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PHYLOGENETIC ANALYSIS OF THE RAPANINAE (NEOGASTROPODA: MURICIDAE)

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ABSTRACT

The generic level revision and phylogenetic analysis of the gastropod subfamily Rapaninae Gray, 1853 (Prosobranchia: Neogastropoda: Muricidae), presented here is based primarily on gross anatomy (female and male reproductive systems, alimentary system, mantle cavity organs), radular, opercular, and protoconch morphology, and shell ultrastructure. Results reveal that Rapaninae includes most members previously allocated to the Thaidinae Jousseaume, 1888. The type species of most recognized rapanine genera were studied for character selection. Eighteen characters were determined for cladistic analyses, and results were compared with additional data derived from egg capsule morphology and biogeographic data.

The cladistic analyses show (1) that the former Thaididae/nae of authors is polyphyletic and should be divided into two (monophyletic) groups; (2) that family status is not justified for either of these groups; (3) that *Rapana* Schumacher, 1817, is monophyletic with Thaidinae, resulting in synonymization of Thaidinae Jousseaume, 1888, with Rapaninae Gray, 1853; and (4) that several genera belonging to the Rapaninae merely deserve subgeneric status.

The genera *Nucella* Röding, 1798, *Forreria* Jousseaume, 1880, *Trochia* Swainson, 1840, *Acanthina* Fischer von Waldheim, 1807, and *Haustrum* Perry, 1811, are placed in Ocenebrinae Cossmann, 1903 (*sensu* Kool, 1993); the genera *Cymia* Mörch, 1860, *Rapana* Schumacher, 1817, *Stramonita* Schumacher, 1817, *Concholepas* Lamarck, 1801, *Dicathais* Iredale, 1936, *Drupa* Röding, 1798, *Plicopurpura* Cossmann, 1903, *Pinaxia* H. & A. Adams, 1853, *Nassa* Röding, 1798, *Vexilla* Swainson, 1840, *Cronia* H. & A. Adams, 1853, *Morula* Schumacher, 1817, *Thais* Röding, 1798, *Purpura* Bruguière, 1789, and *Mancinella* Link, 1807, are placed in Rapaninae. The taxa *Vasula* Mörch, 1860, *Tribulus* Sowerby, 1839, and *Neorapana* Cooke, 1918, are allocated subgeneric status under *Thais*.

> "My Thais, thou hast seen these filthy snails crawling towards thee with their sticky sweat . . . Thais, Thais, Thais, . . . say if thou wilt go mad with them!"
>
> Anatole France, *Thais*

INTRODUCTION

Of all large littoral prosobranchs, none are more conspicuous and perplexing, in a taxonomic sense, than gastropods belonging to the Rapaninae ["Rapananina"] Gray, 1853, herein shown to include Thaidinae Jousseaume, 1888 (*sensu* Kool, 1989 [= Thaididae/nae of authors, *in partem*]). Rapaninae, *sensu* Kool (from this point onward referred to as Rapaninae), comprises many more genera than Rapaninae of authors. The Rapaninae is a group of predatory gastropods belonging to the family Muricidae Rafinesque, 1815, in the superfamily Muricoidea (*sensu* Ponder, 1973; see below). Most rapanines live in the rocky intertidal zone where wave energy can be very high, but members of the genus *Rapana* Schumacher, 1817, are subtidal. Rapanines prey on a variety of invertebrates (mollusks, polychaetes, crustaceans, cnidarians, etc.; see Kool, 1987), although some are known to eat invertebrate and vertebrate carrion; some species are specialists (for example, coral feeders), others generalists.

My initial assumption was that the Thaididae/nae of authors was a conglomerate of disparate taxa, and that para- and polyphyly would be rampant in this "waste-basket group." Although Rapaninae have been commonly used for ecological (Spight, 1982; J. D. Taylor, 1984), environmental (Bryan et al., 1986, 1987), genetic (Palmer, 1984, 1985), physiological (Carriker et al., 1978), and biochemical (Huang & Mir, 1972) research, little is known about the evolutionary relationships among the members of this group, and its status among other muricid groups.

Taxonomic History

Traditionally, the superfamily Muricoidea Rafinesque (*sensu* Thiele [as Muricacea]) has been divided into several different families (Table 1). Ponder (1973) advocated inclusion of several other neogastropod families in Muricoidea, so that Muricoidea, *sensu* Thiele, is almost equivalent to Muricidae, *sensu* Ponder. Unless noted otherwise, Muricidae will herein be equivalent to Muricoidea, *sensu* Thiele.

Members of the Muricidae have an often spiny shell, usually bearing a distinct, sometimes long, anterior siphonal canal. An anatomical feature shared by most Muricidae is the accessory boring organ, located in the foot, and used for chemically dissolving shell material. Naticids have an accessory boring organ as well, but this structure apparently has arisen independently in these distinct groups. Most Muricidae have a long radular ribbon with a row of tri- or pentacuspid rachidian (central) teeth, each of which is flanked by a lateral tooth. The tri- and pentacuspid rachidian morphology occurs also in other Neogastropoda (for example, Buccinidae).

The taxonomy and phylogeny of the Muricidae have been in a state of confusion for over two centuries. Taxonomic problems within the Muricidae as a whole impede our understanding of all groups within this taxon. For example, due to the vague boundaries of many higher muricid taxonomic groups, the limits of lower groups can not be set, and *vice versa*. Keen (1971a: 35) pointed out that "distinctions between subfamilies within the Muricidae are not always clear-cut, . . ." This taxonomic confusion results in a lack of understanding of the phylogeny of all muricid groups.

Familial and subfamilial arrangements of Muricidae differ greatly among authors. A selection of arrangements and authors is listed in Table 1. For example, Cossmann (1903) recognized five subfamilies within the Muricidae: Ocenebrinae [authors and dates of taxa given in Table 1], Muricinae, Trophoninae, Typhinae, and Rapaninae; he included the members of the Thaididae/nae of authors in the Purpuridae as a separate family. Thiele (1929) included two families, Muricidae and Magilidae, and did not list subfamilies. Wenz (1941) included the same two families, but subdivided the Muricidae into the subfamilies Muricinae, Rapaninae, Columbariinae, and Drupinae (Thaidinae of authors). Keen (1971a) recognized the families Muricidae, Columbariidae, Sarganidae, Coralliophilidae, Moreidae, and Thaididae; she subdivided the Thaididae into the subfamilies Thaidinae, Rapaninae, and Drupinae. Radwin & D'Attilio (1971) subdivided the Muricidae into the families Muricidae, Columbariidae, Rapanidae, Coralliophilidae, and Thaididae. Ponder (1973) reduced the number of superfamilies in the Neogastropoda and included the Buccinidae, together with 16 other families in the Muricoidea, and followed Cossmann's (1903) subdivision of the Muricidae. Harasewych (1983) showed that the Columbariinae do not belong within the Muricidae but instead in the Turbinellidae. Ponder & Warén (1988) include in Muricidae the subfamilies Muricinae, Thaidinae (with Rapaninae in synonymy), Coralliophilinae, Sarganinae, and Moreinae.

Of the subgroups of the Muricidae, the group formerly known as Thaidinae (or as Thaididae) Jousseaume, 1888 (original spelling "Thaisidae"), is probably the most problematic and in need of comprehensive revision. Some authors have ranked this group as a subfamily, but many have given it family rank (Table 2).

The family-subfamily controversy is a result of a poor understanding of genus-level relationships within the Rapaninae and of relationships between Rapaninae and the other muricid taxa. The generic allotment for the many rapanine species is highly suspect, as generic boundaries are usually ill-defined. Many muricid genera of uncertain status have been placed in Thaididae/nae of authors, resulting in a conglomerate of disparate taxa. Therefore, Thaididae/nae of authors, as well as other higher level muricid taxa, are probably para- and/or polyphyletic.

Taxonomic controversy in Rapaninae has existed from the time when rapanine genera were given their own group-name and ranking. Menke (1828) considered the group as a superfamily and used the name Purpuracea. Swainson (1835, 1840) referred to this group as Purpurinae. Broderip (1839) ranked this group as a family (Purpuridae). The family-level designation has been used most frequently since then. Other synonyms of Thaididae/nae of authors (and thus *in partem* of Rapaninae, as defined herein) are Concholepadidae Perrier, 1897, Purpuradae Leach, 1852, Thaisidae Jousseaume, 1888, Thaidae Cooke, 1919, Drupinae Wenz, 1941, Thaisidinae Kuroda & Habe, 1971, Thaidiidae Atapattu, 1972, and Nucellinae Kozloff, 1987 (see also Ponder & Warén, 1988).

The oldest rapanine generic name still in use is *Purpura,* introduced by Martini (1777). Due to the controversial history of *Purpura* (see treatment of this genus), Keen (1964) proposed that the names "Purpurinae," "Purpuridae" and "Purpuracea" be placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology and to place Thaididae Suter, 1913 [originally as "Thaisidae"], on the Official List of Family-Group Names in Zoology. The Commission acted on this petition (ICZN, Opinion 886, 1969) and placed Purpuracea Menke, 1828, and Purpurinae Swainson, 1840 [*sic*], on the Official Index of Rejected and Invalid Family-Group Names in Zoology. Furthermore, the Committee ruled that Purpuridae Broderip, 1839, and Thaididae Suter, 1913, be placed on the Official List of Family-Group Names in Zoology, and that Purpuridae not have priority over Thaididae. From this point on, the stem "Thaid-" has been used most frequently for rapanine gastropods (Table 2). As Cernohorsky (1980) pointed out, "Thaididae Jousseaume, 1888" (originally as "Thaisidae"), predates Thaididae Suter. Lehtinen (1985) petitioned to adopt the original spelling "Thaisidae" to avoid homonymy with the spider family Thaididae Lehtinen, 1967 (based on the genus *Thaida*), but later withdrew his petition.

Convergent Shell Morphology: Roots of Taxonomic Discord

The main reason for the plethora of taxonomic arrangements for muricid groups is a poor understanding of muricid phylogeny. The characters on which all past taxonomic schemes were based are distilled primarily from external shell morphology. These features are readily visible but are misleading in that they may have resulted from convergent and/or parallel evolution.

Many authors have pointed out that shell morphology within a species is effected by environmental influences. For example, environmental factors often dictate a particular shell shape and/or shell color. Examples of ecophenotypic variation are given in a number of papers on muricids (primarily the genus *Nucella* Röding) (Agersborg, 1929; Vermeij, 1975, 1979, 1982; Palmer, 1979; Vermeij & Currey, 1980; Etter, 1987; Day, 1990) and on other gastropod groups as well (S. J. Gould, 1971; Cain, 1981). If environmental influences are strong enough to cause high selection pressures at the population level, selective forces may also have caused convergence in shell shape among species. Shell convergence among species may thus be high, and any taxonomic scenario for the Muricidae (or other gastropod group) based exclusively or primarily on shell morphology is therefore highly suspect.

Evidence for the phenomenon of environmentally induced shell shape is given for the species *Nucella lapillus.* Cooke (1895, 1919) pointed put that stunted, short-spired specimens of *Nucella lapillus* occurred in very exposed areas, whereas those living in sheltered areas had high-spired shells with a relatively small aperture. Crothers' (1973, 1974) studies on ecophenotypic variation of *Nucella lapillus* reported similar results to those of Cooke. Kitching et al. (1966) were able to demonstrate experimentally that morphs of *Nucella* with wide apertures had greater adhesive power to cling to intertidal rocks than did the morphs with narrower apertures, thus providing an adaptationist explanation for variation in shell shape. Other characters derived from shell morphology correlating with environment are color patterns and sculpture (Agersborg, 1929; Etter, 1987).

Besides wave action, other environmental influences reportedly play a role in determining aspects of shell morphology. Balaparameswara Rao & Bhavarayana (1976) were able to correlate shell morphology statistically in *Drupa tuberculata* with temperature and desiccation at different intertidal levels. Moore (1936) suggested that the great intraspecific variation in shell shape in *Nucella* was due to differential feeding. Bandel (1984) showed that juveniles of *Stramonita haemastoma floridana* would "change" into typical *Stramonita haemastoma* in the laboratory when food levels were kept artificially high. Hallam (1965) stated that a combination of such factors as food availability, salinity, oxygen concentration, temperature, turbidity and agitation, and population density, may induce stunting in mollusks and other invertebrates. Wilbur & Owen (1964), in discussing allometric growth in mollusks, pointed out that growth rates for different bodily parts may not be equal; thus shell shape may depend on a snail's age. They also showed that this allometry may also partly be due to a combination of several environmental factors.

Many authors have noted population differences in shell shape in different muricidae

TABLE 1. Important supraspecific taxonomic arrangements for muricids.

Authors	Taxonomic Names
Fischer, 1887	PECTINIBRANCHIATA
	MURICIDAE Rafinesque, 1815
	CORALLIOPHILIDAE Chenu, 1859
Cossmann, 1903	RHACHIGLOSSA
	MURICIDAE Rafinesque, 1815
	MURICINAE Rafinesque, 1815
	OCENEBRINAE Cossmann, 1903
	TROPHONINAE Cossmann, 1903
	(incl. *Forreria*)
	TYPHINAE Cossmann, 1903
	RAPANINAE Gray, 1853
	PURPURIDAE Broderip, 1839
	(incl. thaidines *s.l.*)
	CORALLIOPHILIDAE Chenu, 1859
Thiele, 1929	MURICACEA Rafinesque, 1815
	MURICIDAE Rafinesque, 1815
	MAGILIDAE Thiele, 1925
Wenz, 1941	MURICACEA Rafinesque, 1815
	MURICIDAE Rafinesque, 1815
	RAPANINAE Gray, 1853
	(incl. *Forreria*)
	COLUMBARIINAE Tomlin, 1928
	MURICINAE Rafinesque, 1815
	DRUPINAE Wenz, 1941
	(incl. thaidines *s.l.*)
	MAGILIDAE Thiele, 1925
	(incl. *Coralliophila*)
Radwin & D'Attilio, 1971	MURICACEA Rafinesque, 1815
	COLUMBARIIDAE Tomlin, 1928
	RAPANIDAE Gray, 1853
	CORALLIOPHILIDAE Chenu, 1859
	THAIDIDAE Jousseaume, 1888
	MURICIDAE Rafinesque, 1815
	(7 subfamilies)
Keen, 1971a	MURICACEA Rafinesque, 1815
	MURICIDAE Rafinesque, 1815
	(5 subfamilies)
	COLUMBARIIDAE Tomlin, 1928
	CORALLIOPHILIDAE Chenu, 1859
	MOREIDAE Stephenson, 1941
	SARGANIDAE Stephenson, 1923
	THAIDIDAE Jousseaume, 1888
	THAIDINAE Jousseaume, 1888
	DRUPINAE Wenz, 1941
	RAPANINAE Gray, 1853
Ponder, 1973	MURICACEA Rafinesque, 1815
	MURICIDAE Rafinesque, 1815
	(not specific about subfamilial divisions)
	BUCCINIDAE Rafinesque, 1815
	(and all other rachiglossate families usually attributed superfamilial status by other authors).
Golikov & Starobogatov, 1975	MURICOIDEA Rafinesque, 1815
	MURICIDAE Rafinesque, 1815
	VASIDAE H. & A. Adams, 1853
	CORALLIOPHILIDAE Chenu, 1859
	THAIDIDAE Jousseaume, 1888

(*continued*)

TABLE 1. (*Continued*)

Ponder & Warén, 1988	MURICOIDEA Rafinesque, 1815 MURICIDAE Rafinesque, 1815 MURICINAE Rafinesque, 1815 (incl. Trophoninae, Ocenebrinae, etc.) THAIDINAE Jousseaume, 1888 (incl. Rapaninae) CORALLIOPHILINAE Chenu, 1859 MOREINAE Stephenson, 1941 ?SARGANINAE Stephenson, 1923

TABLE 2. Ranking of thaidine higher taxa since Thaididae, Jousseaume, 1888, by a selection of authors.

Family Rank

Thaididae: Hedley, 1918; Iredale, 1937; Clench, 1947; Korobkov, 1955; Pchelintsev & Korobkov, 1960; Keen, 1964, 1971a, b; Strausz, 1966; Jung, 1969; Radwin & D'Attilio, 1971, 1972; Vokes, 1972; Golikov & Starobogatov, 1975; Petuch, 1982; Harasewych, 1984; Kensley, 1985; Kensley & Pether, 1986.
Thaisidae: Suter, 1909; Stewart, 1927; Iredale & McMichael, 1962; Powell, 1961; Miller, 1970.
Thaidiidae: Atapattu, 1972.
Thaidae: Cooke, 1919.
Purpuridae: Cossmann, 1903; Lamy, 1928; Coomans, 1962; Settepassi, 1971; Abbott, 1974.
Concholepadidae: Perrier, 1897.

Subfamily Rank

Thaidinae: Cernohorsky, 1969; Beu, 1970; Emerson & Cernohorsky, 1973; Rosewater, 1975; Rehder, 1980; Emerson & D'Attilio, 1981; Fujioka, 1985a.
Thaisidinae: Kuroda & Habe, 1971.
Drupinae: Wenz, 1941; Hertlein, 1960.
Purpurinae: Baker, 1895.

No Separate Rank

Muricidae: Thiele, 1929; Demond, 1957; Barnard, 1959; Arakawa, 1962, 1964, 1965; D. W. Taylor & Sohl, 1962; Habe, 1964; Wu, 1965a, 1968, 1973, 1985; Habe & Kosuge, 1966; Maes, 1966, 1967; Powell, 1979.

but have not investigated causes for this phenomenon (Colton, 1916, 1922; Kincaid, 1957; Berry & Crothers, 1968, 1970; Cowell & Crothers, 1970; Hoxmark, 1970, 1971; Largen, 1971; Crothers, 1973; Spight, 1973).

If environment causes high intraspecific variation in shell morphology among muricids (and gastropods generally), it is not surprising that convergence in shell shape is a frequently recognized phenomenon (Ponder, 1973; Davis, 1979; Signor, 1982; Harasewych, 1984; Vermeij & Zipser, 1986). Similar shell shapes may have evolved in response to similar environmental pressures. Thus, convergence in shell shape is probably the major underlying cause of existing taxonomic controversies within the Thaididae/nae of authors and other muricid groups.

Of course, shell morphology can be deceiving in another way as well: major differences in external shell morphology may obscure a possibly close phylogenetic relationship, which may—as does convergence—result in paraphyletic and/or polyphyletic groups.

Radular morphology is the second-most utilized criterion on which to base taxonomic groups within Thaididae/nae, although radular characters are almost always used in conjunction with shell characters (Cooke, 1919; Thiele, 1929; Clench, 1947; Arakawa, 1962, 1964; Wu, 1968, 1985; Radwin & D'Attilio, 1971, 1972, 1976; Emerson & Cernohorsky, 1973; Bandel, 1984; Harasewych, 1984; Fujioka, 1985a). Troschel (1866–1893) used radular characters as the sole basis for his classification.

Although radular characters in Thaididae/nae of authors and other molluscan groups have been applied cautiously, no studies correlating radular morphology and diet existed until recently (Kool, 1986, 1987) to indicate whether this caution is justified. Radular characters have often been regarded as, at most, moderately indicative of relationship, in particular, when radular characters do not show congruence with shell shape. In this case, adaptationist explanations usually have been invoked in which radular morphology is postulated to have evolved as a direct response to dietary habits (Arakawa, 1964 [Rapaninae, *sensu* Kool]; Wu, 1965a [Rapaninae, *sensu* Kool]; Powell, 1964 [Turridae]; see also Kool, 1987). Several authors (Arakawa, 1962; Radwin & D'Attilio, 1972; Wu, 1973; Fujioka, 1985a) have mentioned intrageneric differences in rapanine radulae. However, the generic determinations and boundaries used by these authors were based on shell morphology, and may therefore have been invalid. A detailed investigation by Kool (1987) showed that radular morphology in Thaididae/nae of authors does not reflect diet, but is indicative of relationships as determined by anatomy [i.e. "soft" anatomy (not including radula)].

However, some degree of caution is necessary. Sexual dimorphism in radulae has been reported for several genera in Rapaninae: *Nassa* (Maes, 1966), *Drupella* Thiele, 1925 (Arakawa, 1957; Fujioka, 1982), *Morula* (Fujioka, 1984), and *Cronia* (Fujioka, 1984). Furthermore, Fujioka (1985a) and DiSalvo (1988) observed ontogenetic changes in the radulae of several rapanine species, and Fujioka (1985b) also found seasonal aberrant radular formation to occur in two species of rapanines. Anatomical [not including radula] data are probably the most reliable morphological data in reflecting phylogenetic relationships. Molluscan anatomists, such as Ponder (1973), Houbrick (1978), and Davis (1979), have demonstrated the importance of anatomical characters as opposed to characters derived from external shell morphology in establishing phylogenetic relationships. It is now generally agreed that a reliable phylogenetic explanation for any molluscan group must be based on a robust set of anatomical data.

In contrast to the vast amount of descriptive data on shell morphology, and the information available on radular morphology, very little is known about the anatomy of representatives of the Rapaninae and other muricid groups. Most anatomical studies are either superficial or focus on specific aspects of anatomy, such as the alimentary system (Righi, 1964; Wu, 1965a; Rajalakshmi Bhanu et al., 1980, 1981a, b; Carriker, 1981; Shyamasundari et al., 1985), and the reproductive system (Houston, 1976; Gallardo & Garrido, 1989; Srilakshmi, 1991). Haller (1888) presented an exceptionally detailed anatomical study of *Concholepas concholepas* (Bruguière, 1789), and anatomical information is also available on *Nucella* (Fretter, 1941; A. Graham, 1941, 1949; Fretter & Graham, 1962; Harasewych, 1984; Houston, 1976) and *Acanthina* (Wu, 1985). Several anatomical reports exist on a variety of other muricid taxa, e.g. *Urosalpinx* Stimpson, 1865 (Carriker, 1943, 1955; Carriker et al., 1972), *Trophon* Montfort, 1810 (Harasewych, 1984; E. H. Smith, 1967), and *Rapana* (Chukhchin, 1970).

Recently, the topic of "imposex" (the occurrence of male characters in female snails, in particular a penis) in especially Muricidae has received much attention (Féral, 1976; Hall & Feng, 1976; Bryan et al., 1986, 1987; Gibbs & Bryan, 1986; Gibbs et al., 1987; Bright & Ellis, 1990). The occurrence of imposex is highly correlated with environmental pollution by the chemical tributyltin.

Another non-conchological feature that may be of use in unraveling evolutionary relationships among rapanines is egg capsule morphology. Aspects of egg capsule morphology of muricids have been treated by a variety of authors (Lebour, 1936, 1945; Amio, 1957; Ganaros, 1958; D'Asaro, 1966, 1970a, b, 1986; Gohar & Eisaway, 1967; Bandel, 1976; Tirmizi & Zehra, 1983). The most comprehensive work on muricid egg capsules to date is by D'Asaro (1991), who provided detailed descriptions for the egg capsule morphology of a wide variety of muricids.

Hypothesis and Objectives

The working hypothesis of this study is that a classification resulting from cladistic analyses of a data set of primarily anatomical characters will differ from all previous classifications and will be far more reliable than those based primarily on shell shape. The new classification will reveal which names and taxonomic levels should be applied to one or more monophyletic groups.

This first comprehensive comparative anatomical study will establish a testable inference of phylogeny and a classification not only for those taxa traditionally included in Thaididae/nae of authors, but also for other muricid groups. Furthermore, this study will provide a framework onto which other taxa can be added more easily, after limits of different taxa are set by identification of synapomorphies.

MATERIALS AND METHODS

Compilation of Morphological Data

Eighteen type species (herein referred to as: *Concholepas concholepas* (Bruguière, 1789), *Cronia amygdala* (Kiener, 1835), *Cymia tecta* (Wood, 1828), *Dicathais orbita* (Gmelin, 1791), *Drupa morum* Röding, 1798, *Haustrum haustorium* (Gmelin, 1791), *Mancinella alouina* (Röding, 1798), *Morula uva* (Röding, 1798), *Nassa serta* (Bruguière, 1789), *Neorapana muricata* (Broderip, 1832), *Nucella lapillus* (Linnaeus, 1758), *Pinaxia versicolor* (Gray, 1839), *Purpura persica* (Linnaeus, 1758), *Stramonita haemastoma* (Linnaeus, 1767), *Thais nodosa* (Linnaeus, 1758), *Tribulus planospira* (Lamarck, 1822), *Vasula melones* (Duclos, 1832), and *Vexilla vexilla* (Gmelin, 1791)], and one "non-type species," *Plicopurpura patula* (Linnaeus, 1758), representing 19 genera usually placed in Thaididae/nae of authors, were studied in detail (Appendix 1). Two additional type species, also usually placed in Thaididae/nae of authors, *Acanthina monodon* (Pallas, 1774) and *Trochia cingulata* (Linnaeus, 1771), were examined on a relatively low number of characters. Furthermore, one taxon belonging to Rapaninae of authors, *Rapana rapiformis* (Born, 1778), one taxon belonging to Muricinae, *Muricanthus fulvescens* (Sowerby, 1841), and one taxon *incertae sedis, Forreria belcheri* (Hinds, 1844), were examined in detail. A fossil taxon *incertae sedis, Ecphora* cf. *quadricostata* (Say, 1824) was examined also. Twenty-four of the above-mentioned taxa (excluding *Ecphora*) were subjected to cladistic analyses performed with Hennig86 (Farris, copyright 1988).

The database used to address questions of muricid phylogeny consisted primarily of anatomical data, but also included data from protoconch, operculum, radula, and shell ultrastructure. Anatomical variation within and among species was determined by dissection of a variety of specimens. Most voucher specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; others are at the Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A, or at the Museum of Comparative Zoology, Harvard University.

Field work was done at many geographical locations throughout the Pacific and western Atlantic oceans, and in numerous habitats (rocky intertidal, mangrove forest, etc.), allowing a variety of ecological and behavioral observations (spawning, feeding, etc.). When possible, egg capsules of rapanine species were collected during spawning.

Both living and preserved specimens were used in this study. Living animals were maintained in tanks of running sea water and observed periodically before being sacrificed. Prior to dissection, animals were de-shelled using a vice and observed under a dissecting microscope. In some cases, a 7.5% isotonic solution of magnesium chloride was used to relax the animals. Snails were dissected while alive to observe color patterns, gross anatomy, and variability within an individual in structures such as the penial flagellum. Dissected animals were fixed in 10% formalin and preserved in 70–75% ethyl alcohol for further study. Preserved museum material was frequently in poor condition due to incomplete penetration of preservative, and provided limited information.

Some morphological data were obtained from histological sections and study of critical-point dried specimens using the Hitachi S-570 and Cambridge Stereoscan (100 and 250 MK II) scanning electron microscopes at the U.S. National Museum of Natural History. Pallial gonoducts were embedded in paraffin and sectioned at 7, 10, or 15 micrometers, depending on the size of the animal and the degree of detail desired. They were normally stained using triple PAS stain, although other stains (Masson's and Cason's) were occasionally used.

Morphological analyses resulted in a data matrix consisting of 18 characters and 64 character states. These characters were derived from the protoconch, shell ultrastructure, operculum, mantle cavity complex (ctenidium, osphradium), female and male reproductive and alimentary systems, and radula, and were used in cladistic analyses.

Because shell morphology is known to be under the influence of environmental selection pressures, the only shell characters used in cladistic analyses are those taken from larval shells and shell ultrastructure (see below).

Description of Characters

A variety of philosophies advocate different ways of choosing and justifying characters for reconstructing phylogeny. For example, some authors argue that characters displaying parallelism and convergence should not be used in phylogenetic analyses. However, parallelisms and convergences are only recognizable after analyzing the branching patterns of phylogenetic trees. Once a convergence between two synapomorphic states is recognized, the character in question should not be automatically discarded, because this results in loss of information and may in addition, lead to a reduction in resolution within or among branches of the tree. A case of homoplasy should be re-evaluated and re-divided into character states (perhaps with the tree topology based on other characters as a guide). Parallelisms and convergences, after all, provide valuable information about the manner in which different organisms adapt to possibly similar circumstances, and they indicate areas requiring more detailed study. Furthermore, those character states of a (partially homoplasious) character that are not homoplasious and occur only once in a branching sequence are additional synapomorphies and add to the resolution of the cladogram.

Convergence in external shell morphology is known to exist. Judging from the variety of taxonomic arrangements based on shell morphology and the results from the cladistic analyses presented herein, characters taken from the external morphology of the teleoconch have been very misleading in assessing relationship (Kool, 1988b). For these reasons, I have not included characters from external shell morphology in the cladistic analyses presented here. However, with the obtained branching pattern as a frame work, "good" (i.e. reflecting relationship) characters from the external shell morphology can be identified and could be added in future analyses.

Most of the characters used in the phylogenetic analysis are anatomical characters (reproductive system, alimentary system [excluding radula], mantle cavity, etc). The other characters were taken from shell ultrastructure, protoconch, operculum, and radula.

To avoid duplication of figures (often only differing in only minor details [e.g. length of accessory salivary glands]), general lay-outs of different morphological systems with their individual structures and organs are illustrated in Figures 3 (whole animals, reproductive systems, alimentary system, mantle cavity organs), 4 (female reproductive system), 5 (male reproductive system), and 6 (rachidian tooth).

I made no *a priori* assumptions about the validity of characters in reconstructing phylogeny and used all characters analyzed. For example, a variety of authors has expressed suspicion about the phylogenetic significance of radular morphology in a variety of groups (Kool, 1987). Diet is often suspected to be the driving force behind the evolution of radular characters. Although this may be true for some groups, the matter has never been thoroughly investigated. I have shown elsewhere (Kool, 1987) that there is very little correlation between radular morphology and dietary habits in rapanine gastropods, but that high correlation is present between relationship (based on anatomy) and radular morphology. The results of this study (Kool, 1987) show that inclusion of radular characters is indeed justified for reconstructing phylogeny and that characters, which were often assumed *a priori* to be under the influence of environmental factors and thus non-reflective of relationship, need testing against an independent data set (reflecting phylogeny) prior to unqualified prejudice against that particular suite of characters.

The list of characters follows the sequence in which these characters are described in each species.

Protoconch: Most of the protoconchs (and, where possible, the embryonic shell) were described from scanning electron micrographs, but a few descriptions were based on published drawings. Whorls, seen in apical view, were counted from the end of protoconch II spiraling inward. In some cases, the exact number of whorls could not be given due to poor preservation of the protoconch. Most data were derived from SEM micrographs of a single specimen, but other data from light microscopy were frequently added.

Characters:

1. Number of whorls and sculpture
    - (a) multispiral (more than two and a quarter whorls); sculptured (e.g. Figs. 10D, 19C)
    - (b) paucispiral (fewer than two whorls); smooth (e.g. Figs. 15C, 28C)
    - (c) multispiral; smooth (e.g. Fig. 9C)
    - (d) paucispiral; sculptured (e.g. Fig. 23D)
2. Transition into teleoconch
    - (a) outward-flaring lip (e.g. Fig. 10D, E)
    - (b) smooth transition (e.g. Fig. 26B, C)

Shell Morphology: Shell measurements (height and width) were taken from large adult specimens in the USNM collection and do not represent maximum sizes. Height was measured from the apex (tip of earliest whorl) to the most distal point of the anterior siphonal canal, or apertural lip, whichever yielded the highest number; aperture height includes the apertural lip. Shell width is defined here as the distance between the apertural lip (or close to it to avoid inclusion of spines or knobs) and the other side of the body whorl (not including spines or knobs). Percentage measurements of the body whorl and aperture are relative to total shell height, and percentage is rounded off to a whole number and a multiple of five. A consistently present incision in the posteriormost portion of the apertural lip was considered as a posterior siphonal canal. A large number of museum lots was examined for color descriptions.

Shell ultrastructural data were obtained using scanning electron microscopy. Shell fragments of at least two specimens (depending on ambiguity or difficulty of interpretation of data) provided data on the kinds and combinations of shell layers. Fragments were cut out from the central region of the apertural lip with a diamond saw at some distance (about one-half of a whorl away) from the apertural lip edge, and broken collabrally. The fracture surfaces were observed and the different layers identified. In some cases, the fracture surface was polished; this process facilitates recognition of the different layers.

In the descriptions of the ultrastructure of the shells, the layers are listed in consecutive order beginning with the innermost layer (adjacent to the animal). All layers described for any of the taxa treated herein are present in, for example, *Purpura;* Figure 18F can be used for general reference. An approximate range for the thickness of each layer is given relative to all shell layers combined.

Characters:

3. Calcitic outer layer
   (a) absent (e.g. Figs. 13F, 24D)
   (b) present, thick > 25% of total (e.g. Figs. 15G, 26F)
   (c) present, thin < 20% of total (e.g. Figs. 8G, 25D, 18F, e)
4. 45° innermost aragonitic layer
   (a) absent (e.g. Fig. 25D)
   (b) present (e.g. Figs. 14E, 11G, H, 18F, a)

Operculum: In the descriptions of the opercular morphology, terms such as "bracket-shaped" and "arch-shaped" are used to describe the shape of growth lines on both the outside surface, referred to as "free surface" and the inside surface, referred to as "attached surface." In older specimens, the bracket-shaped growth lines often lose their horizontal portions, resulting in growth lines running straight from top to bottom. The terms "left side" and "right side" (on either surface) are used in reference to an operculum with its apex situated upward (the apex actually being the posteriormost end of the operculum). The vertical position of the nucleus varies among taxa; the description "in center right" denotes a nucleus located midway on an imaginary line running from the apex to the lower end of the operculum. The size of the operculum corresponds closely to the size of the shell aperture (given in shell description), unless noted otherwise. No notation of color and color patterns was made; color often reflects the age and thickness of the operculum and varies among individuals of the same species.

Character:

5. Morphology of operculum (shape, position of nucleus)
   (a) operculum ovate; terminal nucleus in lower right (Fig. 1A)
   (b) operculum D-shaped, upper end rounded; lateral nucleus in lower right (Fig. 1D)
   (c) operculum D-shaped, tapered at lower end, and with S-shaped left (adjacent to columella) edge; lateral nucleus in lower right (Fig. 1F)
   (d) operculum inverted tear-shaped; lateral nucleus in lower right (Fig. 1B)
   (e) operculum D-shaped; lateral nucleus in center right (Fig. 1C)
   (f) operculum ovate-elongate, tapered at lower end; lateral nucleus in upper right (Fig. 1E)

Foot and Mantle Cavity: The anatomical descriptions are given as follows. In a first paragraph, most of the external characteristics are listed (coloration and morphology of tentacles [e.g. Fig. 3B, t], head-foot region, kidney [e.g. Fig. 3B, C, k], hypobranchial gland [e.g. Fig. 3B, C, hg], nephridial gland [anteriorly of the kidney; usually visible on left side of live animals]), followed by data on accessory boring organ and (for females) ventral pedal gland (e.g. Fig. 4A, B, abo, pg).

The second and third paragraphs treat the osphradial and ctenidial morphologies (e.g. Fig. 3D, os, ct). The length of the osphradium

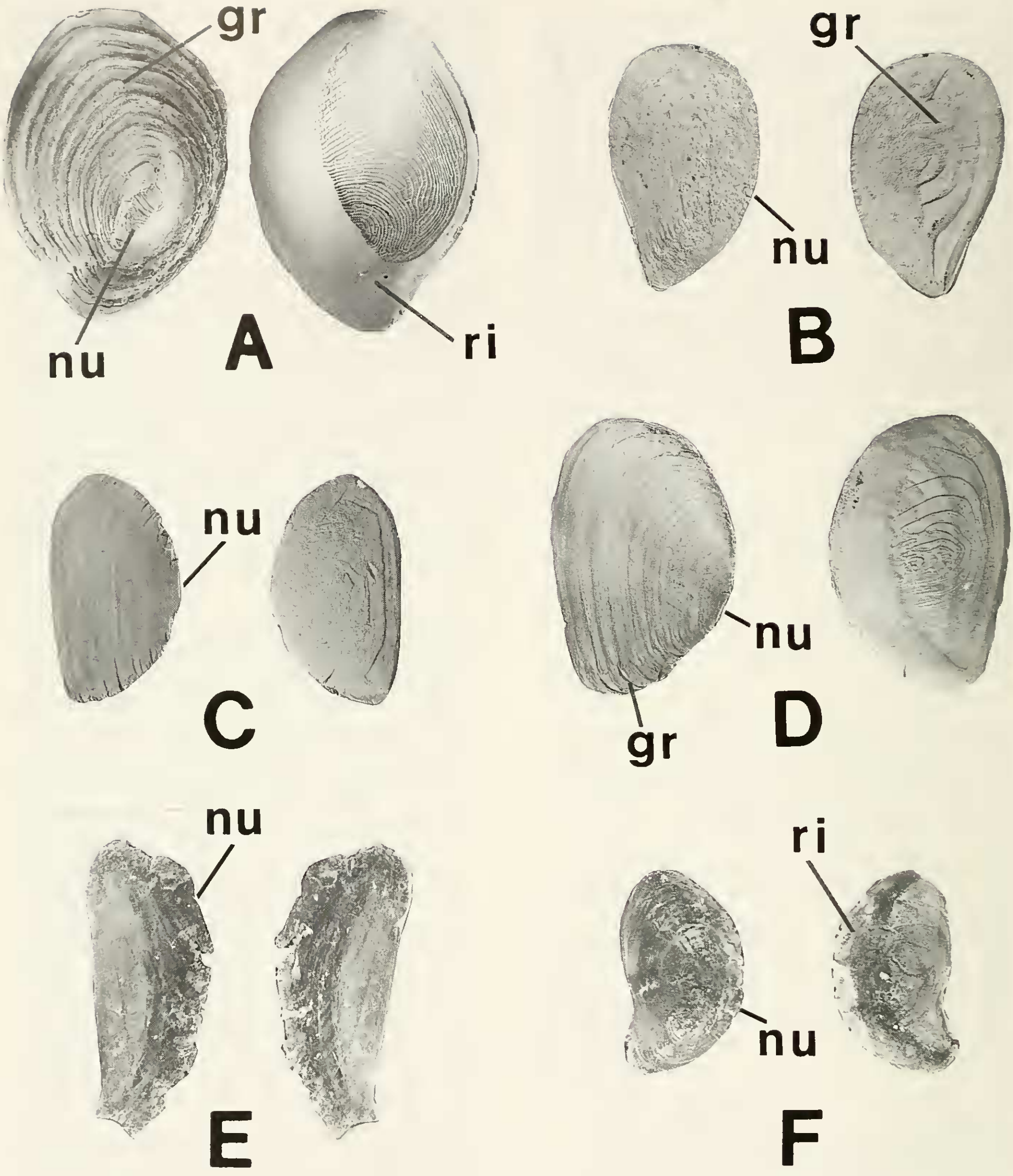


FIG. 1. Morphologies of muricid opercula, showing free surface (facing to the outside) and attached surface (facing inside), respectively. A, *Muricanthus fulvescens.* B, *Rapana rapiformis.* C, *Thais nodosa.* D, *Forreria belcheri.* E, *Vexilla vexillum.* F, *Cronia amygdala;* gr, growth lines; nu, nucleus; ri, rim of callus.

is measured from the posteriormost end (Fig. 3D, pos) to the anteriormost tip (Fig. 3D, ant) along the central axis separating both pectins. Similarly, the length of the ctenidium (gill) is measured along the ctenidial efferent blood vessel (Fig. 3D, cv). Absolute measurements are not given; only relative size (osphradium vs. ctenidium). The term "symmetrical in shape" is used rather than "symmetrical" because although there often is symmetry along the longitudinal (central) axis in the overall shape of both pectins, in none of the taxa examined was the number of osphradial lamellae equal between the left and the right

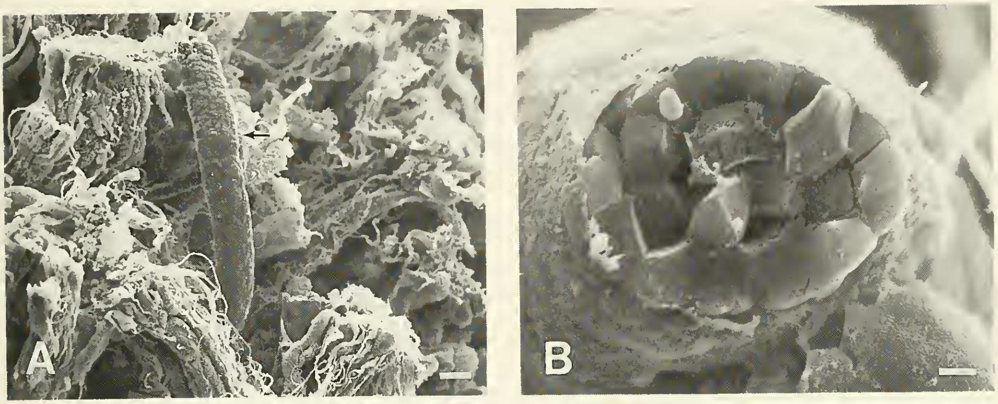


FIG. 2. Rod structures located in hypobranchial gland of *Morula nodulosa*. A, surface of hypobranchial gland with rod structure in center (arrow), SEM (bar = 20 μm). B, cross section through rod structure, SEM (bar = 2 μm).

pectin; the right pectin (directly adjacent to the ctenidium) consistently bears (about 25%) more lamellae than the left one. The general shape of the ctenidium (usually elongate half-moon-shaped [Fig. 3D, ct], or D-shaped) and osphradium (usually ovate-elongate) with left (Fig. 3D, los) and right pectins, is variable at least within some taxa, as is the morphology and number of individual lamellae of both organs. The edge of the ctenidial lamella adjacent and parallel to the support rod is referred to as the ventral edge (Fig. 3D, lr); the other free edge as the lateral edge (Fig. 3D, le). The size of the ctenidial lamellae is described as a relation between width and depth (the latter term was chosen over "height" because the lamellae *in situ* hang down).

Characters:

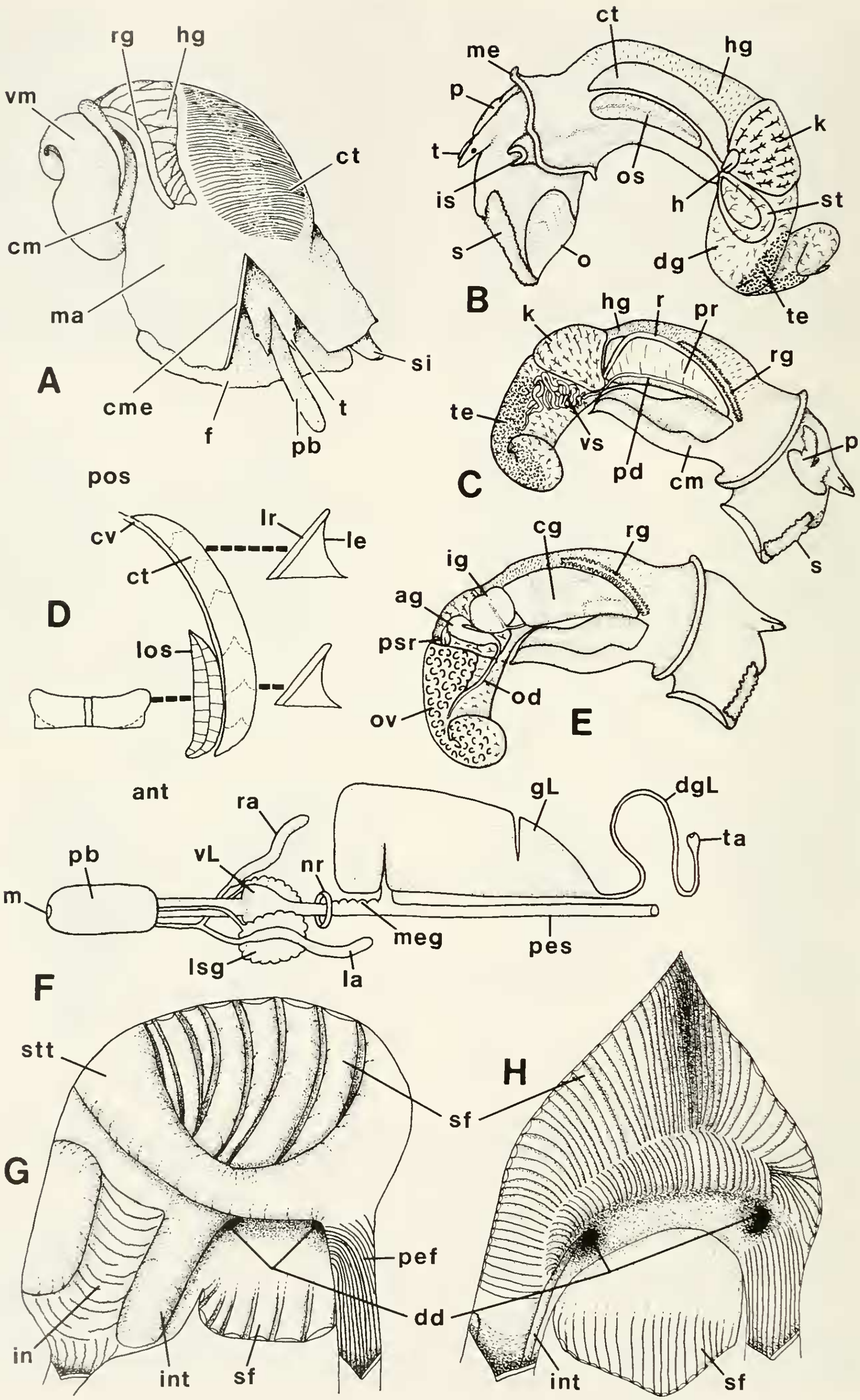
6. Rodlike structures in hypobranchial gland
   - (a) absent
   - (b) present (Fig. 2A, B)
7. Ventral pedal gland and accessory boring organ
   - (a) sharing one duct (e.g. Fig. 4B)
   - (b) having separate ducts (e.g. Fig. 4A)
   - (c) accessory boring organ absent
8. Osphradial length relative to ctenidial length
   - (a) osphradial length less than one-half ctenidial length
   - (b) osphradial length at least one-half ctenidial length

Female Reproductive System: The reproductive organs of the female pallial gonoduct are listed and described in the same order in which the dissections were made (anterior to posterior), beginning with the vaginal opening and the vagina (Fig. 4C, v), followed by the bursa copulatrix (Fig. 4C, bc), capsule gland with left and right lobes (Figs. 3E, cg, 4C, lc, rc), ventral channel (Fig. 4C, vc), ovi-sperm duct (connecting capsule gland with albumen gland; Fig. 4E–H, osd), ingesting gland (Fig. 3E, ig), albumen gland (with or without posterior seminal receptacles; Figs. 3E, ag, 4E–H), and the gonad (Fig. 3E, ov).

Characters:

9. Bursa copulatrix
   - (a) sacklike, separate from lumen of capsule gland (Fig. 4C, bc)
   - (b) continuous with capsule gland (Fig. 4D, bc)
10. Posterior seminal receptacles around albumen gland
   - (a) absent (Fig. 4F, G)
   - (b) 1–3 with duct branching off ovi-sperm duct (Fig. 4E, psr)
   - (c) many (usually at least 7 or 8) (Fig. 4H, psr)
11. Morphology of albumen gland
   - (a) diverticulum of oviduct (Fig. 4F)
   - (b) arch-shaped, elongate (Fig. 4G)
   - (c) staff-shaped (Fig. 4E)
   - (d) omega-shaped, roundish (Fig. 4H)

Male Reproductive System: Descriptions of the organs of the male reproductive system follow the same format as those of the female system. The penis (Figs. 3B, C, p, 5A–F, l) is described, followed by the penial vas deferens (Fig. 5A, B, D, pvd), cephalic vas defer-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ens, prostate (Figs. 3B, pr, 5G, H), prostate duct (Fig. 3B, pd), seminal vesicles (Fig. 3C, vs) and the testis (Fig. 3B, C te). The term "large" as referred to penis size is to be taken relative to tentacle size; a penis which measures more than twice the size of the tentacles is referred to as "large." Changes in penial morphology within the same individual are a common phenomenon in most species. The penis can be extended or condensed, and its shape can thus be altered. In a relaxed state, however, the penial shape does not vary much among individuals of the same species. Penial variation in living specimens facilitated evaluation of penial shapes in preserved specimens.

Characters:

12. Morphology of penis
    (a) elongate, gradually tapering (Fig. 5A)
    (b) straight to lightly curved, with pseudo-papilla (Fig. 5B)
    (c) strongly recurved, with large side lobe (Fig. 5E, I)
    (d) strongly recurved, club-shaped (Fig. 5F)
    (e) strongly recurved, with flagellate pseudo-papilla (Fig. 5D)
    (f) slightly recurved, gradually thinning to flagellate morphology (Fig. 5C)
13. Morphology of penial vas deferens
    (a) duct well developed, semi-closed by interlocking lateral ridges (Fig. 5A, pvd)
    (b) duct minute, open, adjacent to posterior edge of penis
    (c) duct minute, semi-closed by loosely overlapping ventral and dorsal sides of penis; adjacent to posterior edge of penis (Fig. 5B, pvd)
    (d) coiling duct within a larger duct (duct-within-a-duct system) (Fig. 5D, pvd)
14. Morphology of vas deferens of prostate (pallial vas deferens)
    (a) open to mantle cavity in posterior portion (Fig. 5H, prv)
    (b) closed to mantle cavity (Fig. 5G, prv)

Alimentary System: The alimentary system (exclusive of radula) is treated in two paragraphs; one for structures of the anterior portion of the alimentary system (Fig. 3F), such as the proboscis (pb), accessory salivary glands (ra, la), salivary glands (lsg), valve of Leiblein (vL), mid-esophageal glandular folds [on portion of mid-esophagus between nerve ring (nr) and duct to gland of Leiblein; meg], gland of Leiblein (gL), the other for the posterior structures, such as the stomach (e.g. Fig. 3G, H), rectal gland (Fig. 3C, E, rg), and anal opening. Size references for the accessory salivary glands are relative to shell height (see below). Size of the proboscis is given relative to the size of the gland of Leiblein ("large" translates into almost equal in size to gland of Leiblein). The portion of the mid-esophagus containing glandular folds is referred to as "long" when it stretches from the nerve ring to the duct to the gland of Leiblein. The posterior blind duct of the gland of Leiblein is either long (duct longer than one-half of length of gland), or short (duct shorter than one-fourth of length of gland); no intermediate values were found.

The posterior portion of the stomach is herein considered that portion with is directly adjacent to the esophagus; a lateral extension means an extension of the central mixing area of the stomach. The term "stomach typhlosole" (Fig. 3C, stt) refers to the foldlike

FIG. 3. Anatomy of selected rapanines and their organs. A–C, E, whole animals removed from shell. A, *Plicopurpura patula,* male with mantle skirt cut longitudinally to expose head (×1). B, *Morula uva,* male, left side (×10). C, *Morula uva,* male, right side (×10). D, ctenidium and osphradium of *Morula uva,* with lamellae (×15). E, *Morula uva,* female, right side (×10). F, generalized representation of anterior portion of alimentary tract found in rapanines. G–H, morphologies of muricid stomach and intestine, inside views. G, *Nucella lapillus.* H, *Muricanthus fulvescens;* ag, albumen gland; ant, anterior end; cg, capsule gland; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; cv, ctenidial efferent vessel; dd, digestive diverticula; dg, digestive gland; dgL, posterior duct of gland of Leiblein; f, foot; g, gonad; gL, gland of Leiblein; h, heart; hg, hypobranchial gland; ig, ingesting gland; in, intestine; int, intestinal typhlosole; is, incurrent siphon; k kidney; la, left accessory salivary gland; le, lateral edge; los, left osphradial pectin; lr, lamellar support rod (ventral edge); lsg, left lobe of salivary gland; m, mouth; ma, mantle; meg, mid-esophageal folds; nr, nerve ring; o, operculum; od, oviduct; ov, ovary; p, penis; pb, proboscis; pd, prostate duct; pef, longitudinal folds of the posterior esophagus; pes, posterior esophagus; pos, posterior end; pr, prostate; psr, posterior seminal receptacles; r, rectum; ra, right accessory salivary gland; rg, rectal gland; s, sole; sf, folds on gastric wall of stomach; si, siphon; st, stomach; stt, stomach typhlosole; t, tentacle; ta, terminal ampulla; te, testes; vL, valve of Leiblein; vm, visceral mass; vs, vesicula seminalis.

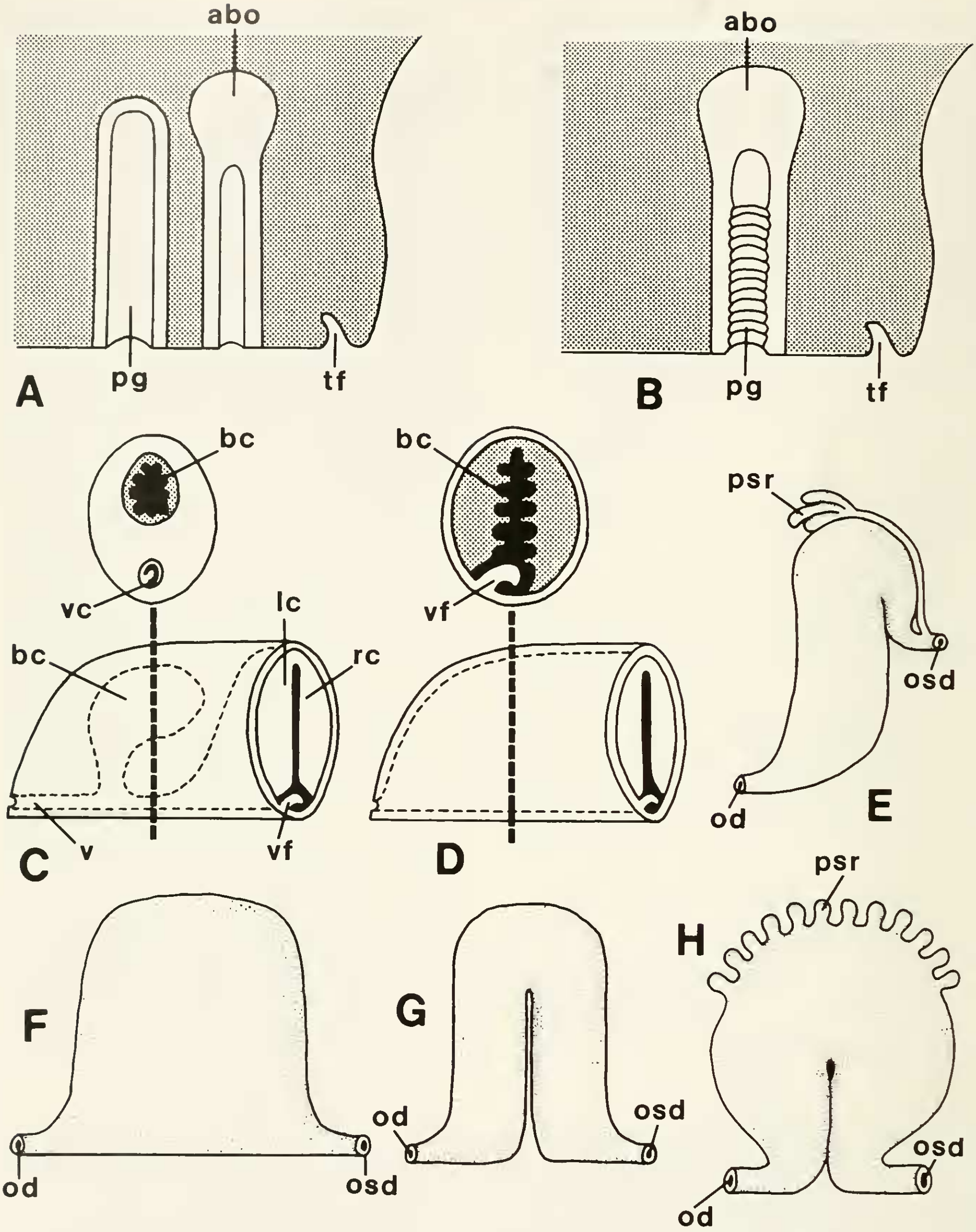

FIG. 4. Morphologies of muricid female reproductive structures. A, B, sagittal cross sections through anterior foot of female, viewed from right. A, ventral pedal gland and accessory boring organ separate (e.g. *Nucella lapillus*). B, ventral pedal gland and accessory boring organ combined (e.g. *Thais nodosa*). C, schematic representation of anterior pallial gonoduct of female non-thaidine muricid (e.g. *Nucella lapillus*), viewed from left, with cross section. D, schematic representation of anterior pallial gonoduct of female thaidine (e.g. *Plicopurpura patula*), viewed from left, with cross section. E–H, albumen gland morphologies in Muricidae, viewed from right. E, e.g. *Morula uva*. F, e.g. *Muricantus fulvescens*. G, e.g. *Nucella lapillus*. H, e.g. *Stramonita haemastoma;* abo, accessory boring organ; ag, albumen gland; bc, bursa copulatrix; lc, left lobe of capsule gland; od, oviduct; osd, ovi-sperm duct; pg, ventral pedal gland; psr, posterior seminal receptacles; rc, right lobe of capsule gland; tf, transverse furrow; v, vagina; vc, ventral channel; vf, ventral flange.

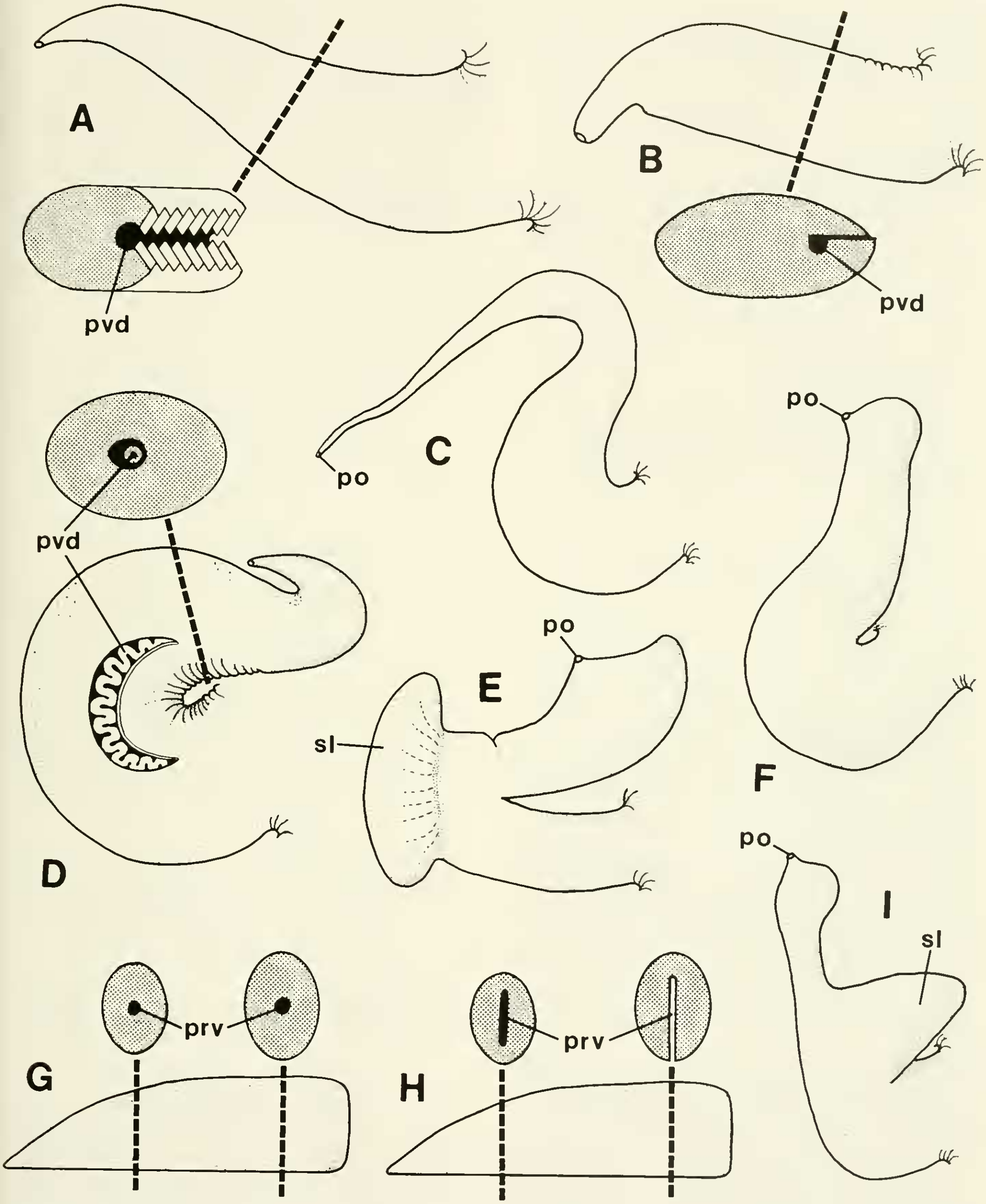

FIG. 5. Morphologies of muricid male reproductive structures. A–F, I, penial morphologies in Muricidae. A, *Muricanthus fulvescens,* with cross section. B, *Nucella lapillus,* with cross section. C, *Nassa serta*. D, *Thais nodosa,* with cross section. E, *Morula uva*. F, *Cymia tecta*. I, *Cronia amygdala*. G–H, schematic representation of prostate morphologies in Muricidae, with cross section. G, e.g. *Thais nodosa*. H, e.g. *Nucella lapillus;* po, penial opening; prv, prostate vas deferens; pvd, penial vas deferens; sl, side lobe.

structure which usually borders the posterior mixing area and can be continuous with what Fretter & Graham (1962) refer to as "typhlosole 2," located in the intestine (e.g. Fig. 3G, int).

Characters:

15. Length of accessory salivary glands
    - (a) right gland minute, nearly undetectable; left one absent
    - (b) both left and right glands very long (nearly one-half of shell height)
    - (c) both glands short to medium (less than one-quarter of shell height; Fig. 3F, la, ra)
    - (d) both glands absent
    - (e) right gland very long (nearly one-half of shell height); left gland absent
16. Length of posterior blind duct of gland of Leiblein
    - (a) duct at least one-half of length of gland (Fig. 3F, dgL)
    - (b) duct shorter than one-half (usually less than one-fourth) of length of gland

Radula: Radulae (2–6 per species) were dissected from living and preserved animals, cleaned in potassium hydroxide, and examined using scanning electron microscopy. For the sake of consistency, only scanning electron micrographs were used for analyzing radular structures. Four micrographs were taken of the central portion of each radular ribbon. The first two micrographs (one including lateral teeth, one excluding lateral teeth) were taken perpendicular to the radular ribbon. The radula was then tilted laterally to an angle of 40° to obtain a lateral view of the morphology of the cusps and denticles on the rachidian tooth. Finally, the radula was tilted laterally to an angle of about 85° to examine the edge of the rachidian tooth and the angles, sizes and locations of its cusps and denticles, in an area from which the lateral teeth had been cut away with a surgical knife.

The morphology of the radula is described starting with the rachidian tooth (Fig. 6B), followed by the lateral teeth. The cusps (three or five) on the rachidian are described beginning with the central cusp (Fig. 6B, cc), followed by the inner lateral denticle (ild), lateral cusp (lc), the marginal area (ma), marginal denticles (d), and marginal cusp (mc). The marginal area is defined as the more or less horizontal area on the outside of the lateral cusp, extending to—if present—the marginal cusp. Size of lateral cusps is given relative to size of central cusp ("nearly equal" translates into 75% or more of central cusp length). The position of the inner denticle(s) is against the base of the inner edge of the lateral cusp, unless noted otherwise. Size of inner lateral denticle is relative to lateral cusp. Size of lateral teeth is given relative to rachidian width. An approximate range of the length of the radular ribbon is given, where available, relative to shell height.

Characters:

17. Orientation of marginal cusp of rachidian tooth
    - (a) marginal cusp absent or in same plane as lateral cusp (and marginal denticles, if present) (e.g. Fig. 7F)
    - (b) marginal cusp in different plane than lateral cusp (forming an approximately 75° angle), on antero-posteriorly widened base (e.g. Fig. 15E, F)
18. Morphology of rachidian tooth
    - (a) marginal area and cusps absent; inner lateral denticle small, free from and between lateral and central cusps; lateral cusps nearly equal in length to central cusp (Fig. 24E)
    - (b) marginal area and cusps absent; inner lateral denticle larger than lateral cusp, free from and between lateral and central cusps; lateral cusps nearly equal in length to central cusp (Fig. 11D)
    - (c) marginal area absent, marginal cusps small; one or more small inner lateral denticles; lateral cusps nearly equal in length to central cusp (Figs. 15E, F, 26D, E)
    - (d) marginal area absent, marginal cusps small; inner lateral denticle small; central cusp much longer than lateral cusps and reclining, forming angle with them (Fig. 8H)
    - (e) marginal area wide, smooth, marginal cusps absent; inner lateral denticle small, free from but adjacent to lateral cusp; central cusp much longer than lateral cusps (e.g. Fig. 8D)
    - (f) marginal area and cusps absent; several faint inner lateral denticles; lateral cusps nearly equal in length to central cusp (Fig. 25C, E)
    - (g) marginal area absent, marginal cusps small; one or more inner lateral denticles; lateral cusps nearly

equal in length to central cusp (e.g. Fig. 7F)

(h) marginal area wide, with multiple denticles and small marginal cusps; inner lateral denticle small; lateral cusps nearly equal in length to central cusp (e.g. Fig. 18D)

(i) marginal area and cusps absent; inner lateral denticle absent; central cusp much longer than lateral cusps (Fig. 11I)

(j) short marginal area with small marginal cusps; inner lateral denticle small or absent; lateral cusps nearly equal in length to central cusp which is wide at base (e.g. Fig. 22E)

Note: both *Neorapana* and *Tribulus* have larger, wider central cusps relative to the lateral cusps. These lateral cusps (those of *Neorapana* without inner lateral denticle) are bent somewhat sideways, which, in the case of *Neorapana,* resulted in the loss of any marginal area. If the Hennig86 program would allow for scoring of more than ten character states, a separate character state would have been assigned to *Neorapana* and *Tribulus.* However, overall morphology of the rachidian tooth strongly suggests homology among the four genera scored for with "(j)."

Taxa which could not be scored due to a limited number of character-state entries in Hennig86 are mentioned below. They are all synapomorphic and thus would not have influenced the topology of the tree.

Nassa—similar to "(i)," but female specimens with small free-standing inner lateral denticle (Fig. 13G).

Plicopurpura—similar to "(i)," but with slit in central cusp (Fig. 17E).

Vexilla—similar to "(i)," but with base of central cusp nearly as wide as rachidian (Fig. 23C).

Phylogenetic Analysis

Data pertaining to the reproductive and alimentary systems, mantle cavity, radula, operculum, protoconch, and shell ultrastructure were subjected to cladistic analyses. No data were derived from external shell morphology.

Three steps were necessary to commence the cladistic analysis: (1) identification of potentially homologous characters; (2) division of each individual character into character states; and (3) polarization of character states, for which the outgroup method was applied. Homology was regarded as two very similar structures with similar location and function.

The outgroup method was used to determine the ancestral state of each character. The outgroup criterion is based on the assumption that character states present in the sister group (outgroup) and the group studied (ingroup) is the plesiomorphic or "primitive" condition (Hennig, 1966). The outgroup method was thus used to determine the "zero state." Use of an outgroup further allows application of the parsimony criterion; it is assumed that the hypothesis based on the lowest number of character changes ("steps") is the best solution for the available data, because it explains the data in the most economical way and is thus based on the smallest number of assumptions made about the evolutionary process (Farris, 1979, 1982; Lipscomb 1984).

The muricine *Muricanthus fulvescens* (Sowerby, 1841) (also known as *Murex fulvescens* and *Hexaplex fulvescens*) appeared suitable to serve as outgroup in the cladistic analysis for several reasons: (1) the Muricinae is a sister group of the Rapaninae; (2) many live-collected and well-preserved specimens were available to provide all data necessary for anatomical studies; (3) most of the structures and characters derived from rapanine anatomy are present also in *Muricanthus* Swainson, 1840, although their "states" may be very different.

The character states of multi-state characters were left unordered; because no realistic assumptions about character state evolution could be made *a priori.* For example, ontogenetic criteria could not be applied because only adult specimens of the type species were available.

Only a few continuous (or quantitative) characters (e.g. size, or numbers) were used due to the arbitrary nature of "cut-off points." Qualitative characters were more easily divided into character states.

The Hennig86 cladistic computer package was used to derive a repeatable, testable, relatively objective, most parsimonious, and most informative hypothesis with the available database. The results herein were very similar to previous results (Kool, 1989) obtained with a slightly different data set using other computer packages (PAUP [Swofford, copyright 1985]; and PHYSYS [Farris & Mickevich, copyright 1985]).

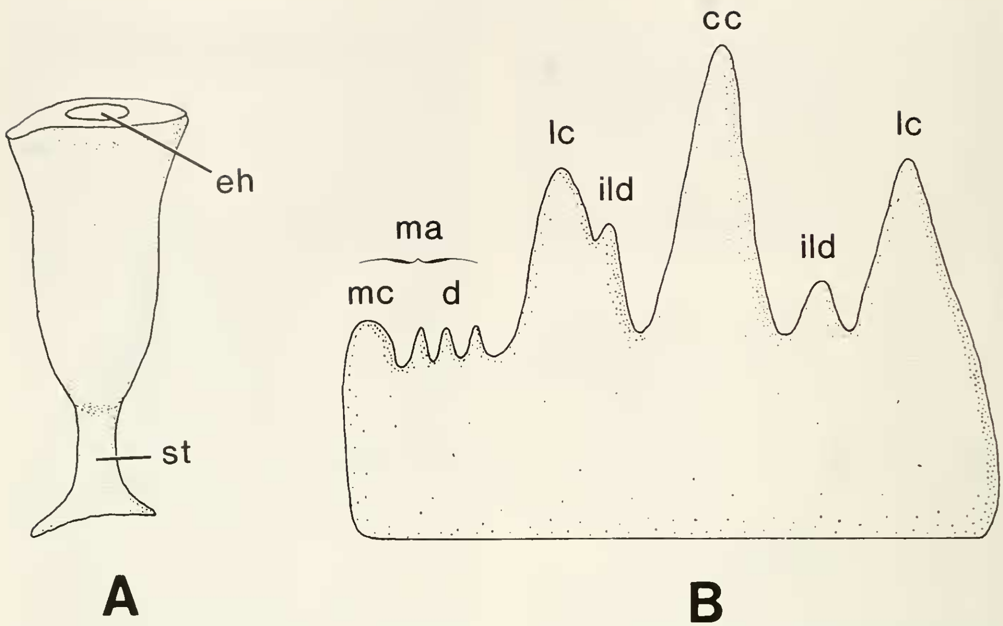

FIG. 6. A, egg capsule of *Cymia tecta,* apical view. B, schematic representation of composite rachidian tooth of muricids (frontal view); cc, central cusp; d, denticles on marginal area; eh, exit hole; ild, inner lateral denticle; lc, lateral cusp; ma, marginal area; mc, marginal cusp; st, stalk.

One of the advantages of using cladistics is the predictive power of the obtained trees. To test the robustness and predictive power of the phylogeny proposed herein, a few taxa were examined on those characters which revealed themselves during early stages of the analysis as unique synapomorphies for certain clades. This "spot checking" allowed for unambiguous placement of taxa for which only limited data were available. Based on the cladistic analyses, limits were set for each group after synapomorphies for each group were identified.

Cladograms never yield a final solution for evolutionary relationships among taxa, and the phylogeny presented herein should be taken only as a testable hypothesis for the evolutionary history of the Rapaninae (as defined herein) and its position in the Muricidae.

RESULTS

The genera formerly included in Thaididae/nae are treated in alphabetical order. A chronologically arranged synonymy of each genus is given, including author, date, page, and information on the type species. The type species of the valid genus name is given, followed by the correct binomen and a synonymy. New combinations are omitted. A "Remarks" section provides for a short discussion of the taxonomic history and placement by different authors (usually including Cossmann, 1903, Thiele, 1929, and Wenz, 1941) of the genus and (type) species.

Different aspects of morphology (protoconch, teleoconch, anatomy, radula, egg capsules) of each species are described in detail, followed by (if available) data on the biology (ecology and geographic distribution) of each taxon. Not treated is the fossil history of each taxon, as most of this information, given by Thiele (1929) and Wenz (1941), is out of date and highly suspect (see "Congruence with Fossil Record").

A less detailed treatment is provided for *Muricanthus fulvescens,* used as outgroup, *Forreria belcheri,* a taxon *incertae sedis,* and *Rapana rapiformis.* I should mention that it was not known initially that *Rapana* was monophyletic with most members of Thaidinae of authors. Only limited data were available on the taxa *Acanthina monodon* and *Trochia cingulata* (both usually included in Thaididae/nae of authors), but the available data were used in the cladistic analysis, partially to test for character robustness.

Although many of the descriptions of the anatomy of the type species are based on dissections of living animals, most observations were based on preserved specimens. Illustrations of anatomy are schematic in order to standardize and elucidate the shared morphologies rather than to show individual idiosyncrasies due to intraspecific variation.

Descriptions of taxa traditionally grouped in Thaididae/nae of authors

Genus *Concholepas* Lamarck, 1801
(Fig. 7A–F)

Concholepas Lamarck, 1801: 69.
Concholepa Deshayes, 1830: 256 (error for *Concholepas*).
Conchopatella Herrmannsen, 1847: 291 (introduced in synonymy).

Type Species: Concholepas peruviana Lamarck, 1801, by monotypy, = *Concholepas concholepas* (Bruguière, 1789); synonym: *Buccinum concholepas* Bruguière, 1789.

Remarks: Lamarck introduced the species *C. peruviana* as type of the genus *Concholepas* and may have considered it a different species from *Buccinum concholepas* Bruguière. More likely, he renamed it without regard for priority to avoid tautonomy (an unpopular nomenclatural procedure at the time). However, these two taxa are synonymous, and the earlier name, *C. concholepas,* has priority. The genus has one living and several fossil representatives (Vokes, 1972; Kensley, 1985). Haller (1888) gave an extensive description of the anatomy of this species, emphasizing the nervous system.

Shell: Protoconch (Fig. 7C, D) squat (wider than high), smooth, of 2.5–3 whorls, with slightly impressed suture, and with outward-flaring lip (DiSalvo, 1988) (eroded from figured specimen) and sinusigeral notch. Teleoconch (Fig. 7A, B) of 2–3 whorls and exhibiting high rate of whorl expansion. Adult shell up to about 125 mm in height, 95 mm in width. Suture slightly impressed, nearly canaliculate on final whorl. Body whorl and aperture reaching beyond apex. Body whorl robust, rounded "patelliform," sculptured with 11–13 spiral, lamellose cords, with one spiral thread in interspaces. Lamellose sculpture most common in juveniles, often persisting in adults. Aperture oval, extending beyond shell spire. Apertural lip with crenate edge, corresponding to spiral cords. Anterior siphonal canal short, wide and open; posterior siphonal canal absent. Columella flat or somewhat concave, continuous with apertural lip, and reaching from beyond apex to anterior siphonal canal. Siphonal fasciole similar to axial ribs but more elevated. One or two labial toothlike structures adjacent to siphonal fasciole on apertural lip. Shell uniformly dark reddish brown; aperture white; columella white, occasionally with light brown areas.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (15–20%); aragonitic layer with crystal planes oriented parallel to growing edge (15–20%); calcitic layer (60–70%) (Fig. 7E).

Operculum: D-shaped (about one-third size of aperture), with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface usually with one bracket-shaped growth line and with callused, glazed rim (about 35–40% of opercular width) on left.

Anatomy: (based on preserved animals only): Cephalic tentacles long and wide. Tentacles a uniform, medium brown. Head-foot and sole of foot mottled dark brown. Mantle edge smooth and following shell contour, with very long brown incurrent siphon. Pinkish and yellow hypobranchial gland positioned within thin, upright, lateral epithelial ridges. Kidney dull caramel brown. Pedal gland in females well developed, with accessory boring organ in proximal portion.

Osphradial length less than one-fourth ctenidial length; osphradial width less than ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, extending farther anteriorly than osphradium. Anterior ctenidial lamellae distinctly wider than deep; posterior lamellae deeper than wide. Lateral and ventral edges of ctenidial lamellae concave, lateral edge occasionally straight. Distal tips of ctenidial support rods extending beyond lateral edge as papillate projections.

Vaginal opening situated on tapering anterior end of pallial oviduct and located directly beneath anal opening. Bursa copulatrix an

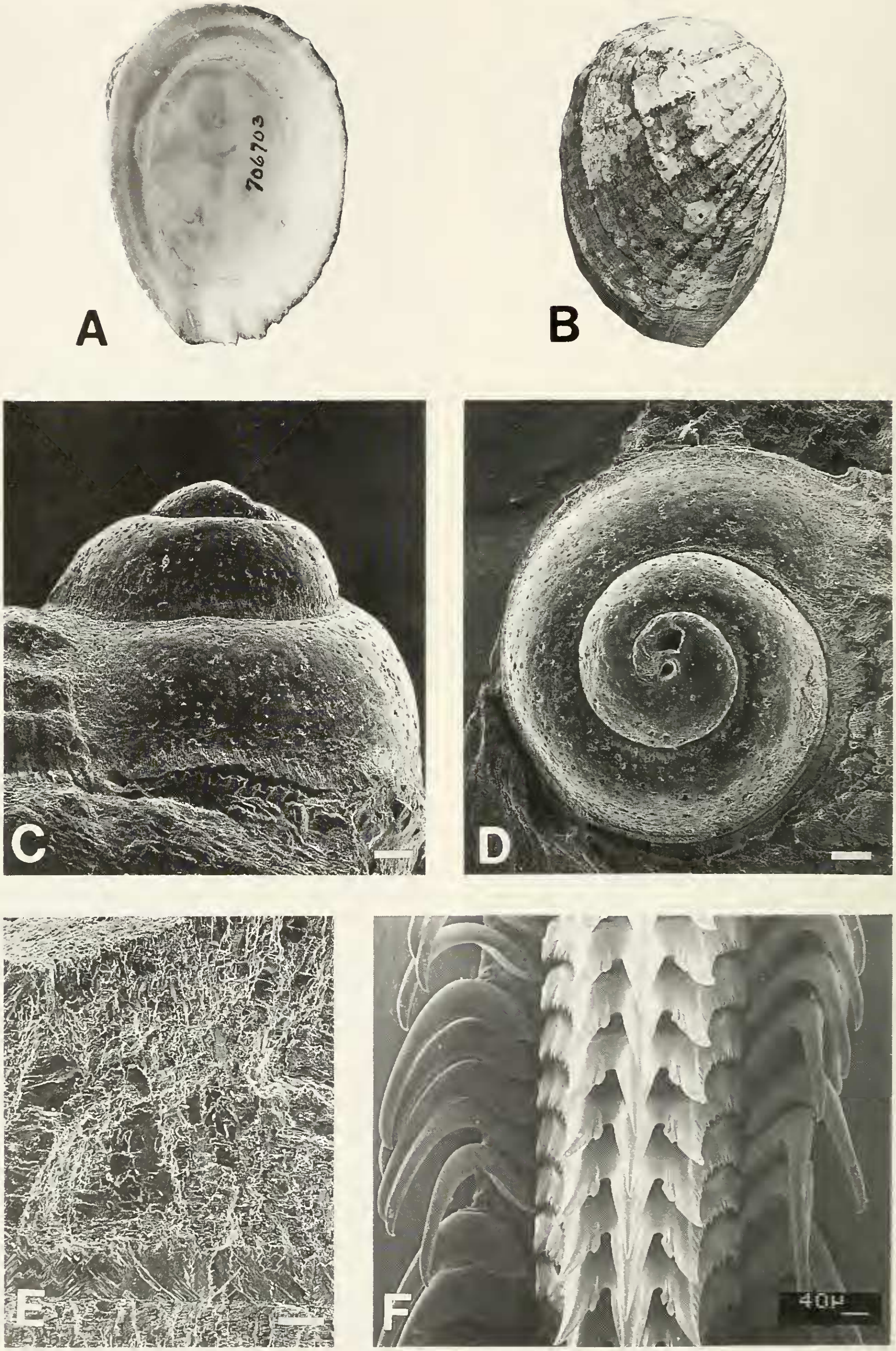

FIG. 7. *Concholepas concholepas*. A, shell (67 mm), apertural view. B, shell (67 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, SEM (bar = 50 μm). F, radula, SEM.

open chamber in interior vagina and open to anterior portion of capsule gland. Posterior part of pallial oviduct with ventral sperm channel consisting of two ventrally located flanges each facing one another and perpendicular to capsule gland lobes. Ventral channel in anterior portion of pallial oviduct very small. Ingesting gland located between capsule gland and albumen gland, continuing on left side of albumen gland, comprising many small, interconnected chambers, and lined with dark yellow epithelium. Seminal receptacles on dorsal periphery of albumen gland small, elongate-oval, white. Albumen gland small, omega-shaped. The external lay-out of the female reproductive system in this species and the species following hereafter is superficially similar to that shown in Figure 3E and in Kool (1988b, fig. 3C).

Penis dorso-ventrally flattened, wide, with large folds along posterior border (in young individual examined), or angular (in older ones). Penial shaft curved, with long and thin flagellate tip. Vas deferens as thin duct-within-a-duct system (Fig. 5D, pvd) occupying about one-fifth of penial width. Prostate gland solid, white, adjacent to spongy, white, rectal wall. Duct of prostate closed off from mantle cavity but sometimes visible through epithelium. Seminal vesicles comprised of small, white or orange outpocketings. Testicular duct following periphery of gonad.

Proboscis whitish, thinner than width of gland of Leiblein. Paired accessory salivary glands of equal length, long, worm-shaped, slightly less than one-half of shell height. Left accessory gland located under and separate from salivary gland but loosely connected to it by many strings of connective tissue. Right accessory gland ventral to proboscis and slightly ventral to salivary glands. Salivary glands cream brown, consisting of many small portions, larger in mass than accessory salivary glands, partially located between gland of Leiblein and proboscis, or partially between nerves emanating from nerve ring. Valve of Leiblein elongate, irregularly shaped, surrounded by salivary glands but not attached to them. Salivary ducts attached some distance from valve of Leiblein; valve separated from nerve ring. Portion of mid-esophagus with glandular folds long; folds well developed. Major portion of posterior esophagus free and looped along side of gland of Leiblein, but small area of posterior esophagus closely attached to it. Gland of Leiblein coiled counterclockwise, forming two folds, brown grey, of hard consistency, with thick outer covering with "interwoven" strings of connective tissue. Blind posterior duct of gland of Leiblein more than one-half length of gland itself. The lay-out of the alimentary system in this and the following species is similar to that shown in Figure 3F.

Stomach buried in digestive gland, with center projecting deep into visceral mass, and with lateral extension. Interior epithelium forms many (about 20) distinct folds, the largest central and perpendicular to typhlosole. Folds on right portion of stomach curve into central fold; folds of left portion perpendicular to stomach typhlosole. One diverticulum present. Stomach typhlosole well developed, continuing onto stomach wall. Intestinal typhlosole wide and shallow. Several minute folds on right side of intestinal typhlosole in intestinal groove. Anal opening distinct, wide, varying from thin- to thick-walled. Anal papilla poorly developed. Rectal gland well developed, green, adjacent to entire length of pallial gonoduct.

Radula: Central cusp on rachidian with wide, somewhat constricted base (Fig. 7F); lateral cusps pointing outward; inner lateral denticle located on base of lateral cusp and one-half its length; several knobby outer denticles on base of lateral cusp; marginal cusp very small. Lateral teeth long, thin, wide-based, nearly total rachidian width.

Egg Capsules: Large, about 20 mm in height (Gallardo, 1973), elongate, slightly curving, with undulating surface, and resting on short, thin stalk, about 1 mm in length. Capsules arranged in clusters, close to one another, each containing up to 13,000 eggs (Gallardo, 1979). Eggs up to 158–160 μm in diameter (Gallardo, 1979).

Ecology: Concholepas concholepas is one of the few rapanine gastropods of direct economic importance and of culinary value to man, who is this species' major predator on the west coast of South America (Castilla & Duran, 1985). Thus, a substantial number of papers have been published on its ecology (Gallardo, 1973, 1979, 1980; Gallardo & Perron, 1982; Castilla & Cancino, 1976; Castilla & Duran, 1985). Egg capsules are usually found in the sublittoral zone; planktotrophic veliger larvae hatch from them probably spending up to several weeks in the plankton before settlement (Gallardo, 1979). Adults live and spawn in the rocky intertidal zone, where they feed on barnacles and mussels (Gallardo, 1979; Kool, 1987). DuBois et al. (1980) reported specimens living at a depth of 40 m. DiSalvo (1988) describes the veliger stages. Beu (1970) suggested that fossil relatives of the Recent species lived in much deeper waters.

Distribution: Eastern Pacific, from central Peru to southern Chile (Beu, 1970; Disalvo, 1988).

Genus *Cronia* H. & A. Adams, 1853
(Fig. 8A–D)

Cronia H. & A. Adams, 1853: 128 (as a subgenus of *Purpura*).

Type Species: Purpura amygdala Kiener, 1835, by monotypy, = *Cronia amygdala* (Kiener, 1835); synonyms: ?*Buccinum avellana* Reeve, 1846; ?*Purpura aurantiaca* Hombron & Jacquinot, 1852; ?*Purpura pseudamygdala* Hedley, 1902.

Remarks: The taxon *Cronia* was introduced by H. & A. Adams (1853: 128) as a subgenus of *Purpura* "Aldrovandus" [correct author: Bruguière, 1789), with one species listed. Cossmann (1903: 68) placed *Cronia* as a section under the subgenus *Polytropalicus* Rovereto, 1899, genus *Purpura*. Dall (1909: 50) allotted *Cronia* to *Thais*. Thiele (1929: 294) and Wenz (1941: 1113) placed *Cronia* as a subgenus under *Drupa*. Fujioka (1985a) and Cernohorsky (1982, 1983) used *Cronia* as a full genus.

The species described below resembles Kiener's (1835) figures of *Purpura amygdala* but appears more similar to Hedley's (1902) figures of *Purpura pseudamygdala.* Kiener's figures of *Purpura amygdala* bear more resemblance to the figures of Hedley's *Purpura pseudamygdala* than to Hombron & Jacquinot's figures of *Purpura aurantiaca,* which is most likely conspecific with *Buccinum avellana* Reeve, 1846. I strongly suspect all four "species" to be geographical or ecophenotypic variants of the same species. Cooke (1919: 107) explained that Hedley restricted the *amygdala* form to the southeast coast of Australia, and introduced *Cronia pseudamygdala* for the "species" from Queensland. Closer examination of the types, ranges of variation, and the anatomy of these four "morphs" is necessary before definite statements on this matter can be made.

Shell: Protoconch tall, conical, smooth, of about four adpressed whorls, and with outward-flaring lip and sinusigeral notch (Hedley, 1902: pl. 29, figs. 4–5). Teleoconch (Fig. 8A, B) of 6–7 adpressed, high-spired, fusiform whorls. Adult shell up to about 30 mm (including 3 mm siphonal canal) in height and 15 mm in width. Body whorl about 65–70% of shell height, rounded, heavily sculptured with five pronounced spiral cords, one of them directly below suture, and with 3–4 fine, delicately lamellose spiral lines at regular intervals from one another, between each pair of major spiral cords. Spiral cords bear 8–9 knobs at regular intervals towards the base. Knobs aligned to form about nine thick axial ribs per whorl. Aperture elongate, about 60% of shell height. Apertural lip slightly thickened, with seven denticles. Anterior siphonal canal well developed, short, deep and semi-closed; posterior siphonal canal absent. Siphonal fasciole well developed, delicately lamellose, free from callus on lower columella. Columella with heavy callus deposition. Shell grey brown; knobs on axial ribs white or light brown; aperture light orange brown, especially on columella and lip edge.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (70–75%) (Fig. 8C).

Operculum: D-shaped, with S-shaped left edge, tapered at lower end, with lateral nucleus in lower right (compare Fig. 1F). Free surface with staff-shaped growth lines; attached surface with about 5–7 arch- and bracket-shaped growth lines and with callused, glazed rim (about 30–40% of opercular width) on left.

Anatomy (based on living and preserved material): Head-foot and siphon brown with green, yellow and white specks, cephalic tentacles long. Mantle edge smooth, following aperture contour; incurrent siphon long. Hypobranchial gland large, perpendicular to mantle wall, with small, thin, black, rodlike structures embedded in it (compare Fig. 2A, B). Kidney green in males, brown in females. Nephridial gland green in females. Pedal gland as simple duct, combined with large accessory boring organ (Fig. 4B).

Osphradial length equal to or slightly more

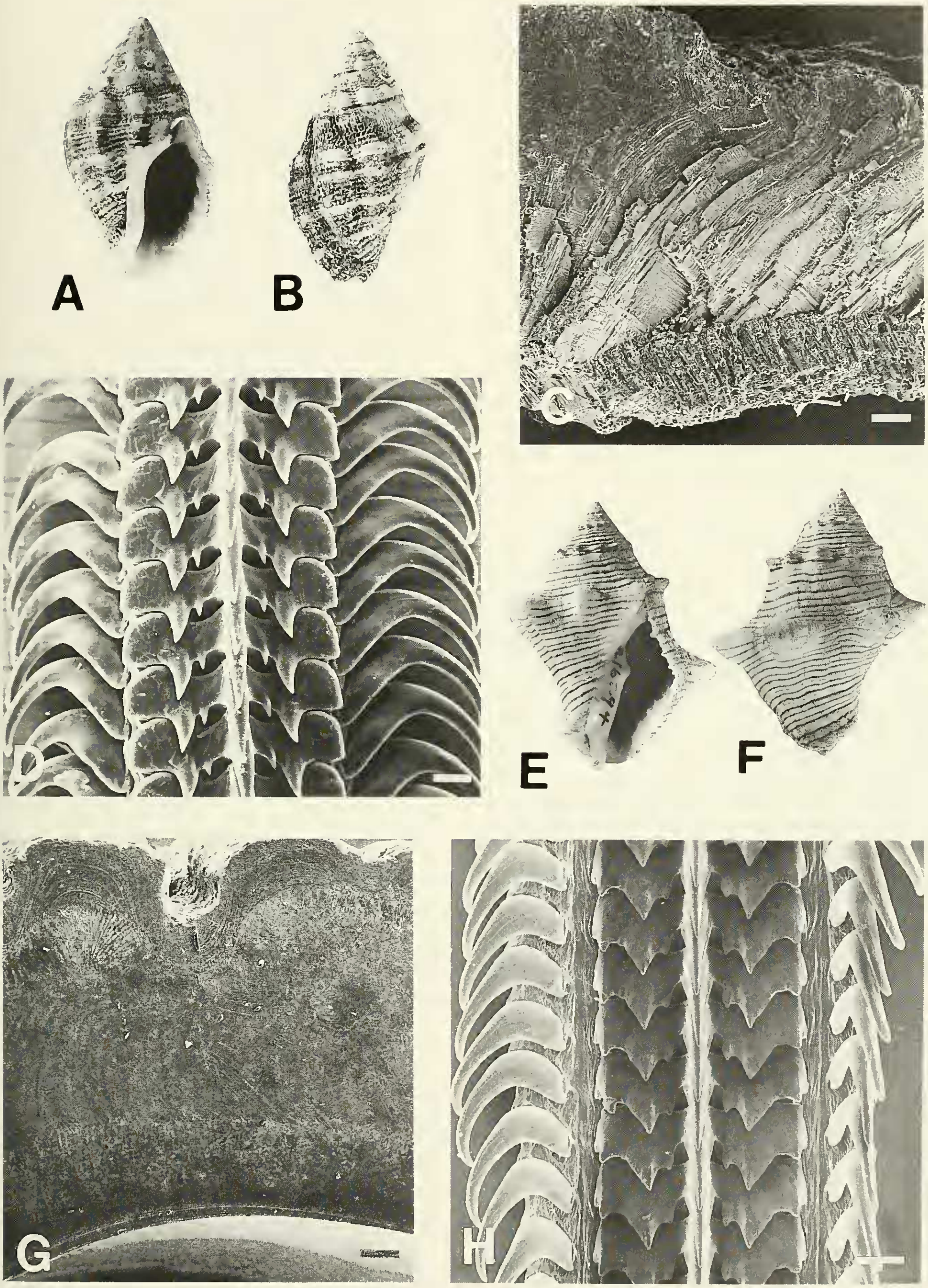

FIG. 8. A–D, *Cronia amygdala*. A, shell (28 mm), apertural view. B, shell (28 mm), abapertural view. C, shell ultrastructure, SEM (bar = 0.10 mm). D, radula, SEM (bar = 30 μm). E–H, *Cymia tecta*. E, shell (55 mm), apertural view. F, shell (55 mm), abapertural view. G, shell ultrastructure, polished surface, SEM (bar = 0.30 mm). H, radula, SEM (bar = 45 μm).

than one-half ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along lateral axis; right pectin wider than left. Osphradial lamellae attached along more than one-half of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae wider than deep. Lateral and ventral edges of ctenidial lamellae usually sharply concave. Distal tips of well-developed ctenidial support rods not extending beyond lateral edge.

Vaginal opening round, situated on distal end of short, attached tube and located below and posterior to anal opening. Bursa copulatrix a dorso-ventral slit, continuous with capsule gland and ventral channel (Fig. 4D). Ventral sperm channel formed by large rolled flange originating from ventral epithelium and lying below both capsule gland lobes. Duct from ovi-sperm duct enters mushroom-shaped, orange-brown (in living animals) ingesting gland, which lies between capsule gland and albumen gland (compare Fig. 3E). Second duct branching off ovi-sperm duct more posteriorly, forming single, elongated, grey seminal receptacle lying above albumen gland (compare Fig. 3E, psr). Sperm apparent from iridescence in receptacle. Albumen gland omega-shaped, usually turned sideways, lying on posterior portion.

Penis with large side lobe (Fig. 5I), basically oval in cross section, with bulbous tip on long thin shaft. Triangular muscular side lobe (Fig. 5I, sl) pointing toward head and tentacles. Penial duct as duct-within-a-duct system (compare Fig. 5D, pvd) occupying about one-fourth of penial width. Testicular duct brown and seminal vesicles weakly developed. Prostate duct closed to mantle cavity. Prostate solid, light brown (in living animals), directly adjacent to rectum, without layer of connective tissue separating both structures. Testis brown.

Proboscis much wider than width of gland of Leiblein. Paired accessory salivary glands both equally short (2 mm), stubby, much less than half of shell height. Left accessory salivary gland embedded in intertwined salivary glands; right accessory salivary gland separated from salivary glands. Salivary glands intertwined, light orange, larger than accessory salivary glands and with granular appearance. Valve of Leiblein elongate, free from salivary glands. Salivary gland ducts attached to esophagus at base of valve of Leiblein, which lies adjacent to nerve ring. Glandular folds on mid-esophagus resulting in slight thickening of mid-esophagus. Duct between esophagus and gland of Leiblein poorly developed. Posterior esophagus separated from gland of Leiblein along entire length. Gland of Leiblein coiled counterclockwise, forming two folds, flat, creamy brown, soft, appearing granular. Posterior blind duct about one-half of length of gland of Leiblein.

Stomach very large, with large sorting area having weak lines arranged randomly. Large, posteriorly located, unciliated area and two digestive diverticula present. Intestinal typhlosole well developed, but stomach typhlosole variable in size. Anal opening inconspicuous; anal gland poorly developed, running dorsally along less than one-half of pallial gonoduct.

Radula: Ribbon length about 20% of shell height (Fig. 8D). Rachidian with long, thin central cusp; lateral cusp with convex inner edge and smooth, concave outer edge; inner lateral denticle small, separate from lateral cusp; large, smooth, horizontal area between lateral cusp and edge of rachidian. Lateral teeth curved, smooth, slightly larger than half the rachidian width.

Egg Capsules: Unknown.

Ecology: Specimens of *Cronia amygdala* were collected on an intertidal offshore coral reef fringing a mangrove forest at Cockle Bay, Magnetic Island, Queensland, Australia. Abe (1983) reported *Cronia margariticola* (Broderip) to be a scavenger, preying upon a wide variety of food items, or feeding on eggs of *Thais clavigera* (Küster).

Distribution: West, north, and east Australia (Eisenberg, 1981) and Pacific Ocean (Cernohorsky, 1972).

Genus *Cymia* Mörch, 1860
(Fig. 8E–H)

Cuma Humphrey, 1797 (rejected work).

Cuma Swainson, 1840: 87 (*non* Milne-Edwards, 1828) [type: *Cuma sulcata* Swainson, 1840, by monotypy, = *Cymia tecta* (Wood, 1828)].

Cymia Mörch, 1860: 97 (replacement name for *Cuma* Swainson; as subgenus of *Rapana*).

Cumopsis Rovereto, 1899: 105 (unnecessary replacement name for *Cuma* Swainson; as subgenus of *Purpura*).

Cyma Rovereto, 1899: 105 (error for *Cymia*).

Type Species: Cuma sulcata Swainson, 1840, by monotypy, = *Cymia tecta* (Wood, 1828); synonyms: *Buccinum tectum* Wood, 1828; *Purpura angulifera* Duclos, 1832.

Remarks: Swainson (1840: 87) placed *Cuma* in the subfamily Pyrulinae, family Turbinellidae, and included only one species, *Cuma sulcata*. Mörch introduced *Cymia* as a replacement name for *Cuma* Swainson, which was pre-occupied, and placed it under *Rapana.* Rovereto (1899: 105) synonymized *Cuma* Swainson with his replacement name, *Cumopsis,* allotted it to *Purpura,* and did not list any other species to be included in this subgenus. Korobkov (1955: 299) considered *Cymia* to be a subgenus of *Thais.*

Shell: Protoconch unknown. (Protoconch of *Cymia brightoniana* Maury "a little more than one whorl" [Jung, 1969: 497]). Teleoconch (Fig. 8E, F) heavy, fusiform, oblong, of 7–8 adpressed whorls, with high spire and shallow suture. Early whorls sculptured with spiral, incised lines. Adult shell up to about 70 mm in height, 50 mm in width. Body whorl about 65–70% of shell height, sculptured with 8–10 large, spinose knobs on periphery of very pronounced, centrally located shoulder of each whorl. Suture adjacent to and following lower contours of these knobs. Twenty-five to 30 deeply incised spiral grooves on body whorl, several crossing knobs. Aperture moderately large, about 70% of shell height. Apertural lip thin, reflecting pattern caused by incised lines. Anterior siphonal canal short, wide, open; posterior siphonal canal poorly developed or absent. Heavy, central fold on columella. Siphonal fasciole curving, well developed, only partially covered by moderate callus layer on fasciole. Shell white, yellow, grey-brown; aperture and columella white to very light orange.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (30–35%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–20%); calcitic layer (15–20%) (Fig. 8G).

Operculum: D-shaped, with strongly concave left edge (to accommodate fold on shell fasciole), with lateral nucleus at center right (compare Fig. 1C). Free surface with bracket-shaped growth lines indented in center; attached surface with about 4–6 arch- and bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on preserved animals only): Cephalic tentacles short, stubby, with black blotches. Head-foot mottled black. Mantle edge crenate (following aperture lip contour). Incurrent siphon protruding farther than mantle edge. Sole of foot with many, primarily laterally crossing, shallow grooves, resulting in pustulate pattern. Pedal gland large, separated from accessory boring organ, but adjacent to it. Small lateral folds on wall of distal part of pedal gland; proximal part smooth. Accessory boring organ large, compact, chamber-shaped, adjacent to pedal gland in females.

Osphradial length less than one-half ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along longitudinal axis; usually wider anteriorly. Osphradial lamellae attached along large portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium, or osphradium extending slightly farther anteriorly. Anterior ctenidial lamellae wider than deep; posterior lamellae deeper than wide. Lateral and ventral edges of ctenidial lamellae variable in shape. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening elongated, located directly below anal opening. Bursa copulatrix between vaginal opening and capsule gland. Vertical flange large, folded, emanating from dorsal wall of bursa. Flange thin, straight, vertical, folded at tip prior to entering capsule gland. Bursa copulatrix continuous with anterior part of capsule gland. Flange minute, folded at 45° angle in most of capsule gland. Large second bursa between capsule gland and small albumen gland of the omega- or arch-shaped type. Ingesting gland with single chamber.

Penis (Fig. 5F) large, thick, strongly recurved, angular in cross section, with terminal papilla. Penial vas deferens tubular, about one-third of penis width. Cephalic vas deferens poorly developed. Prostate gland round in cross section, clearly separated from rectal wall, and with prostate duct closed off from mantle cavity. Posterior sperm storage area small but elongate, running horizontally on border line of gonad and digestive gland, dorsal to prostate.

Proboscis muscular, thick, half as wide as gland of Leiblein. Paired accessory salivary glands very long, thin, of equal length, more than one-half of shell height. Right accessory salivary gland in dorsal right anterior corner of buccal cavity; left gland intertwined with salivary glands between proboscis and gland of Leiblein. Salivary gland mass dorsal, much smaller than accessory salivary glands. Valve of Leiblein elongate, free from salivary gland mass, adjacent to nerve ring. Salivary gland ducts attached to anterior portion of esophagus directly anterior to valve of Leiblein. Midesophageal folds indiscernible. Nerve ring adjacent to thin, long duct joining esophagus and gland of Leiblein. Posterior esophagus adjacent to lower left of gland of Leiblein. Gland of Leiblein spiral, forming two folds oriented antero-posteriorly, dark brown, of hard consistency. Posterior blind duct approximately one-half of length of gland of Leiblein, running into dorsal branch of the afferent renal vein but not reaching kidney.

Stomach U-shaped, but with large posterior widening. Sorting area with 10–15 folds extending over only half its surface. Sorting area adjacent to intestinal typhlosole with minute folds and ridges parallel to it. Two digestive diverticula present. Intestinal typhlosole large. Rectum embedded in spongy tissue. Anal papilla covering anal opening. Rectal gland long and thin; anal opening well developed.

Radula: Ribbon length about 25% of shell height (Fig. 8H). Rachidian tooth with narrow central cusp; central cusp reclining, thus pointing in different direction than lateral cusp; inner lateral denticle nearly united with lateral cusp, which thus appears very wide; outer edge of lateral cusp straight, without denticulation; area between lateral cusp and edge of rachidian narrow, without denticles; wide marginal cusp pointing forward and parallel to lateral extension on rachidian base. Lateral teeth smooth, about three-fourths of rachidian width.

Egg Capsules: About 6 mm in height, elevated on wide stalk 1 mm long (Fig. 6A). Capsule vase-shaped, with oval, flat top; one side more elevated than other (normally continuing gradually in top layer of capsule); exit hole central, oval, located at slightly horizontal tip of capsule. All capsules appearing to be interconnected with basal membrane. Egg capsules examined (ANSP 355766) deposited on free side of operculum.

Ecology: Specimens were found living on intertidal rocks on mud flats, but also on mud among mangrove roots.

Distribution: Eastern Pacific, from Costa Rica to Ecuador (Keen, 1971b).

Genus *Dicathais* Iredale, 1936
(Fig. 9A–F)

Dicathais Iredale, 1936: 325.

Type Species: Buccinum orbita Gmelin, 1791, by original designation, = *Dicathais orbita* (Gmelin, 1791); synonyms: *Buccinum succinctum* Martyn, 1784 (non-binominal); *Purpura textilosa* Lamarck, 1816; *Purpura scalaris* Menke, 1828 (*non* Schubert & Wagner, 1829); *Purpura aegrota* Reeve, 1846; *Dicathais vector* Thornley, 1952.

Remarks: Iredale (1936: 325) removed *succincta* from the genus *Neothias* Iredale, 1912 (type: *N. smithi* Brazier, 1889, by original designation; emended [unjustified] by Iredale to *Neothais* [1915: 473]), recognized *orbita* Gmelin as its valid name and designated *Dicathais orbita* as type of *Dicathais*. Wenz (1941: 1124) synonymized *Dicathais* with *Neothias*.

Controversy exists about the number of *Dicathais* species. Cooke (1919: 97) observed differences between the radulae of "*Thais succincta* (= *orbita*)" and "*T. textilosa.*" These and three other names (*aegrota*, *scalaris*, and *vector*) are now considered to be geographical variants of one another (Phillips et al., 1973; Powell, 1979). The form here described is typical *Dicathais orbita*.

Shell: Protoconch (Fig. 9C, D) low, smooth, of about four adpressed whorls, with outward-flaring lip and sinusigeral notch. Teleoconch (Fig. 9A, B) of 5–6 adpressed whorls. Adult shell up to about 85 mm in height, 60 mm in width. Spire less than one-third shell height. Suture impressed, canaliculate in final whorl. Penultimate and body whorls sculptured with eight, solid spiral cords and with many minute spiral, incised lines; body whorl about 85% of shell height. Aperture large, ovate, about 70–75% of shell height. Apertural lip thin, deeply scalloped due to spiral cords. Interior of apertural lip deeply grooved. Columella rounded or concave, with callus layer more pronounced toward posterior end. Anterior siphonal canal a short but deep notch; posterior siphonal canal absent. Siphonal fasciole curved, about equally, or slightly more ele-

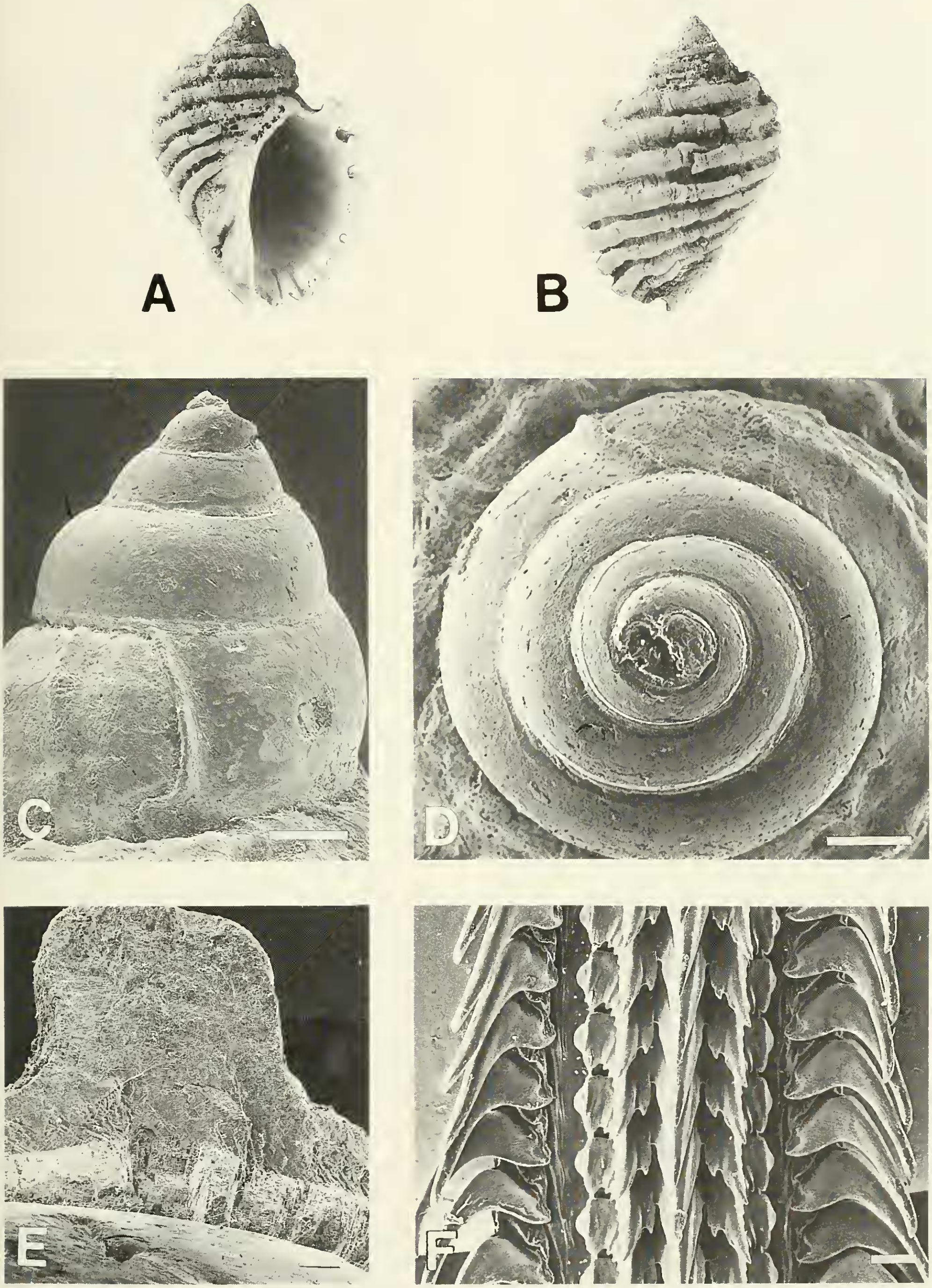

FIG. 9. *Dicathais orbita*. A, shell (58 mm), apertural view. B, shell (58 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.20 mm). D, protoconch, apical view, SEM (bar = 0.20 mm). E, shell ultrastructure, SEM (bar = 30 μm). F, radula, SEM (bar = 40 μm).

vated than spiral cords and adjacent to edge of lower, more heavily callused portion of columella. Shell white yellow to light brown (the latter especially in juveniles); aperture white yellow and columella white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (25–50%); aragonitic layer with crystal planes oriented parallel to growing edge (20–25%); calcitic layer (20–55%) (most pronounced at ribs) (Fig. 9E).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface usually with one bracket-shaped growth line and with callused, glazed rim (about 35–45% of opercular width) on left.

Anatomy: (based on living and preserved animals): Cephalic tentacles long, uniform black. Head-foot mottled black. Mantle edge crenate, following contour line of spiral ribs. Incurrent siphon long, uniform dark brown to black. Accessory boring organ large, dorsal to pedal gland.

Osphradial length about one-half ctenidial length; osphradial width between one-fourth and one-half ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along very small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae usually wider than deep. Lateral and ventral edge of ctenidial lamellae concave.

Vaginal opening a slit, situated on end of thick, tubular, partially detached, distal end of pallial gonoduct, and located directly below anal opening. Bursa copulatrix a channel, with flange, emanating from ventral lobe of capsule gland, forming oval, semi-closed ventral channel. Farther posteriorly ventral lobe of capsule gland absent and ventral channel located under right lobe of capsule gland. Ingesting gland on left of posterior part of capsule gland, with central and many smaller white-walled chambers; gland nearly as large as capsule gland, visible on exterior of body as large, dirty white granular mass. Row of pink, iridescent seminal receptacles on dorsal periphery of albumen gland. Albumen gland shape difficult to discern in adults; morphology in juveniles resembling both omega-shaped and arch-shaped types. Pseudo-penis usually present, either as small appendix or equal in size and shape to penis of male specimens.

Penis large, strongly recurved, with long flagelliform tip, occupying entire space between tentacles and pallial complex, oval in cross section, with penial vas deferens as duct-within-a-duct system occupying nearly total width of penis. Cephalic vas deferens well developed, with internal, meandering tubular duct (similar to penial vas deferens). Prostate solid, dirty white, with accumulations of white granules. Prostate duct as closed tube adjacent to thin, cream-colored rectal wall.

Proboscis very large, unpigmented, slightly less than, or equal in width to, gland of Leiblein. Paired accessory salivary glands long and thin, each adjacent to salivary glands; left accessory salivary gland sometimes slightly longer than right one, and both about one-fourth of shell height. Salivary gland lobes inseparable; right portion under proboscis, extending to right anterior corner of buccal cavity. Valve of Leiblein elongate, irregularly shaped, separate from salivary gland mass. Salivary ducts attached to esophagus some distance from valve of Leiblein. Portion of mid-esophagus with glandular folds long, but poorly developed, except for short, widened section of mid-esophagus; widened section located adjacent to duct of gland of Leiblein. Duct between esophagus and gland of Leiblein thin. Posterior esophagus embedded in lower left side of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, cream-colored, covered with thick, strawlike outer membrane. Posterior blind duct slightly less than length of gland of Leiblein.

Stomach with large posterior projection. Ten to fifteen sizable folds on stomach wall. Two digestive diverticula present. Stomach typhlosole indistinct, poorly developed. Intestinal typhlosole thick, well developed. Long, wide rectal gland dark green. Rectal wall, at minute anal opening, pointing dorsally.

Radula: Ribbon length about 40–45% of shell height (Fig. 9F). Central cusp on rachidian constricted at base; lateral cusps with large inner denticle attached midway; lateral cusps convex on inner edge, concave on outer edge; several faint, knobby, outer denticles on upper half of lateral cusp, and well-developed denticles at base; lateral cusp edge continuing down to well-developed marginal cusp; rachidian base with lateral extension. Lateral teeth nearly equal in length to rachidian width.

Egg Capsules: About 9 mm in height, 6 mm wide, interconnected by basal membrane (Hedley, 1905). Dorsal surface of capsule elongate, rhomboidal, with elongate slit along longest axis. Hedley (1905) found egg capsules of "*Purpura*" *succincta* deposited on the ascidian *Cynthia praeputialis* Heller. Each capsule contains up to about 5,000 eggs (Phillips, 1969).

Ecology: Dicathais orbita has been observed clinging tightly to rocks between large sea-squirts in the low intertidal zone of Botany Bay, Australia. It feeds on the barnacle *Tesseropora rosea* (Kraus) and displays patterns of vertical migration between shelter areas (lower intertidal) and high concentrations of prey (high intertidal) (Fairweather, 1988). It has also been observed on rocks, partially buried in sand. The western Australian variant *Dicathais "aegrota"* lives on limestone reef platforms where wave action is heavy (Phillips, 1969). It therefore seeks shelter in pockets and crevices, or partly buries itself (or gets buried) in the sand. Feeding usually occurs at high tide and at night (Phillips, 1969). Its varied prey consists mostly of mollusks (primarily *Cronia "avellana"*) and malacostracan crustaceans (Phillips, 1969). Large trematode parasites were present in several specimens I collected in Botany Bay (New South Wales, Australia), which had made these individuals sterile. Phillips (1969) also found trematodes in *D. "aegrota."* Some known predators of *Dicathais* are octopods, other *Dicathais* individuals (at least under laboratory conditions), and perhaps crustaceans. *Cronia "avellana"* and Crustacea are known to feed on *Dicathais* egg capsules (Phillips, 1969).

Distribution: Australia, Tasmania, Norfolk Island, Lord Howe Island, Kermadec Island, and New Zealand (Philips et al., 1973; Powell, 1979).

Genus *Drupa* Röding, 1798
(Fig. 10A–E)

Drupa Röding, 1798: 55.

Canrena Link, 1807: 126 [type: *Murex neritoideus* Linnaeus, 1767 by subsequent designation, Iredale, 1937: 256, = *Drupa morum* Röding, 1798, *in partem*].

Sistrum Montfort, 1810: 594 [type: *Sistrum album* Montfort, 1810, by original designation, = *Murex ricinus* Linnaeus, 1758, = *Drupa ricinus* (Linnaeus, 1758)].

Ricinula Lamarck, 1816: 1, pl. 395 [type: *Ricinula horrida* Lamarck, 1816, by subsequent designation, Children, 1823: 56 (as *Ricinula horida*), = *Drupa morum* Röding, 1798].

Ricinulus Lamarck; Chenu, 1859: 174 (invalid emendation for *Ricinula* Lamarck).

Ricimula A. A. Gould, 1855: 263 (error for *Ricinula* Lamarck).

Ricinella Schumacher, 1817: 240 [type: *Ricinella purpurata* Schumacher, 1817, by subsequent designation, Iredale, 1937: 256, = *Drupa rubusidaeus* Röding, 1798].

Pentadactylus Mörch, 1852: 87 [*non* Schultze, 1760, *nec* Gray, 1840] [type: *Murex ricinus* Linnaeus, 1758, by subsequent designation, Baker, 1895: 186, = *Drupa ricinus* (Linnaeus, 1758)].

Drupina Dall, 1923: 303 [type: *Ricinula digitata* Lamarck, 1816, by original designation, = *Drupa grossularia* Röding, 1798].

Type Species: Drupa morum Röding, 1798, by subsequent designation, Rovereto, 1899: 105; synonyms: *Nerita nodosa* Linnaeus, 1758 (*in partem*); *Murex neritoideus* Linnaeus, 1767 (*in partem*); *Ricinula globosa* Martyn, 1784 (non-binominal); *Ricinula horrida* Lamarck, 1816; *Ricinella violacea* Schumacher, 1817; *Ricinula horida* Lamarck, Children, 1823 (error for *horrida*).

Remarks: Cossmann (1903: 68) considered *Ricinula* (= *Drupa*) a full genus. Thiele (1929: 295) subdivided the genus *Drupa* into the subgenera *Drupa* (sections *Drupa, Morula,* and *Drupina*), *Cronia* (sections *Cronia, Morulina, Usilla, Muricodrupa*), *Phrygiomurex, Maculitriton,* and *Drupella.* Wenz (1941: 1113) included the subgenera *Drupa, Morulina, Usilla, Cronia, Muricodrupa, Phrygiomurex, Maculitriton, Morula,* and *Drupella* in *Drupa.* Keen (1971b: 553) placed *Drupa* in the Drupinae. Emerson & Cernohorsky (1973) divided *Drupa* into the subgenera *Drupa, Ricinella* and *Drupina* on the basis of shell morphology.

Shell: Protoconch similar to that of *Drupa grossularia* (Fig. 10D, E), tall, conical, consisting of at least 3.5 adpressed whorls [exact count could not be made from available specimen], with small subsutural plicae, interconnected by three thin spiral ridges, but other-

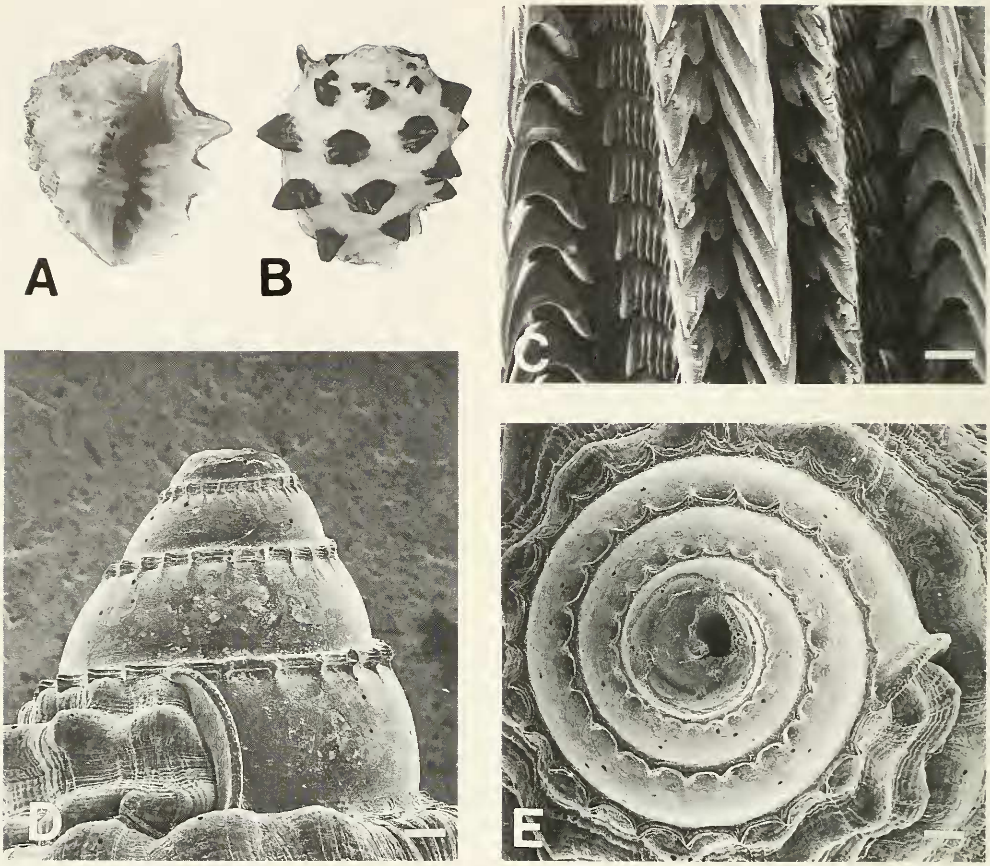

FIG. 10. A–C, *Drupa morum*. A, shell (35 mm), apertural view. B, shell (33 mm), abapertural view. C, radula, SEM (bar = 25 μm). D–E, *Drupa grossularia*. D, protoconch, side view, SEM (bar = 0.10 mm). E, protoconch, apical view, SEM (bar = 0.10 mm).

wise smooth, and with outward-flaring lip; sinusigeral notch covered by teleoconch. Teleoconch (Fig. 10A, B) globose but flat on apertural side, low-spired, of 3–4 adpressed whorls. Adult shell up to about 40 mm in height, 35 mm in width. Body whorl about 85–90% of shell height, dome-shaped, robust, thick, and sculptured with five rows of spiral bands of seven heavy, sometimes spinelike, axially arranged knobs. Largest knobs on second and third row, knobs on fifth row weakest. Thin, lamellose, spiral, microscopic riblets over entire whorl. Aperture about 95–100% of shell height; apertural opening narrow, elongate. Interior of apertural lip heavily callused, with pair of wide teeth, each pair comprising 2–4 denticles; in addition, two weak, separate denticles near anterior siphonal canal; interior of aperture with weak denticles at previous growth intervals. Anterior siphonal canal a short and open notch; posterior siphonal canal absent. Columella heavily callused, curving inward in center, and with three strong columellar teeth. Three to four well-developed knobs on siphonal fasciole. Shell white, knobs dark brown to black; aperture and columella purple.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (0–15%; lacking in some specimens); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–35%); aragonitic layer with crystal planes oriented parallel to growing edge (40–55%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–10%). Presence of calcitic layer questionable.

Operculum: D-shaped, tapered at lower end, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 4–7 bracket-shaped growth lines and with callused, glazed rim (about 35–40% of opercular width) on left.

Anatomy (based on living and preserved animals): Mantle edge, siphon and cephalic tentacles light green with white flecks; distal portion of tentacles dark brown with white tip. Side of foot white with many green dots; sole of foot light green with white specks. Minute accessory boring organ with long duct dorsal to long, thin pedal gland.

Osphradial length slightly more than one-half ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium bending below osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae almost as wide as deep. Lateral edge of ctenidial lamellae concave; ventral edge straight.

Vaginal opening small, elliptical, situated on dorsal side of rodlike, tubular, partially detached extension of pallial gonoduct and located directly below anal opening. Bursa copulatrix consisting of main channel and connecting chamber on right side, the latter continuous with capsule gland. Ventral channel initially located under ventral lobe, farther posterior under right lobe, and formed by large, complex flange with longitudinal ridges. Ventral flange emanating from ventral epithelium. Ingesting gland dark brown, consisting of several small chambers filled with flocculent brown material; located on left side and partially ventral to capsule gland, extending to left side of albumen gland. Seminal receptacles white, located on dorsal periphery of omega-shaped albumen gland.

Penis large, strongly recurved, with small papilla-like tip. Penial vas deferens as duct-within-a-duct system occupying one-fourth of penial width. Cephalic vas deferens a well-developed duct-within-a-duct system. Prostate white, C-shaped in cross section (anteroposterior view), with large C-shaped lumen separating left and right lobes; folded over and under rectum, thus enveloping it. Seminal vesicles yellowish white.

Proboscis long, unpigmented, narrower than gland of Leiblein. Esophagus attached to ventral surface of proboscis by numerous, thin muscle threads. Accessory salivary glands absent. Large paired salivary gland lobes separate; right gland under proboscis; left one dorsal, extending between left side of proboscis and gland of Leiblein. Valve of Leiblein short, separate from salivary glands. Caplike structure present on anterior portion of valve of Leiblein. Salivary ducts attached to esophagus a short distance from valve of Leiblein. Valve of Leiblein adjacent to nerve ring. Glandular folds on mid-esophagus indiscernible. Esophagus directly attached to caramel brown gland of Leiblein. Posterior esophagus embedded along left side of gland of Leiblein. Gland of Leiblein spiral, forming two folds (three "lobes"). Posterior blind duct shorter than gland itself, but larger than one-half of gland length.

Stomach tubular, very elongate; distinct lines or small folds on posterior mixing area, and one diverticulum present. Stomach typhlosole and intestinal typhlosole well developed. Anal opening conspicuous. Rectal gland appearing integrated with hypobranchial gland and separated from rectum by epithelial layer.

Radula: Ribbon length about 30% of shell height (Fig. 10C). Central cusp of rachidian constricted at base; inner lateral denticle on base of lateral cusp attached almost along its entire side; outer edge of lateral cusp straight, lateral denticles absent; six to seven elongate marginal denticles on slightly sloping, narrow marginal edge, with one or two fused with base of lateral cusp; marginal cusp thicker and longer than marginal denticles. Lateral teeth curved, longer than one-half of rachidian width.

Egg Capsules: Unknown.

Ecology: Much information is available on the ecology of several species of *Drupa*. J. D. Taylor (1983) has extensively studied the ecology and in particular the feeding habits of *Drupa* species. Besides general information on feeding habits, species and sizes of prey from different geographic region were listed and discussed (J. D. Taylor, 1983). *Drupa morum* feeds mainly on eunicid polychaetes, such as *Lysidice* sp. (Bernstein, 1970), but occasionally also on *Lepidonotus* sp., *Perinereis* sp. and *Eurythoe complanata* (Pallas) (J. D. Taylor, 1984; Thomas & Kohn, 1985). *Drupa ricinus* feeds on *Dendropoma gregaria* (Thomas & Kohn, 1985).

J. D. Taylor (1971) reported finding *Drupa morum* on the outside of cobbles and boulders, and stated that *Drupa* species tend to live on vertical surfaces. I have found *Drupa morum* living on intertidal limestone benches, where wave action can be very high. Thomas & Kohn (1985) reported three species of *Drupa* living on a windward, seaward platform. *Drupa morum* lives subtidally as well, with individuals reaching a large size in this habitat. Emerson & Cernohorsky (1973) reported *Drupa morum* living at a depth of 40 m. I have collected *Drupa grossularia* at 10 m depth on Niue Island (central South Pacific).

Distribution: Indo-Pacific (between 35°N and 35°S), from Red Sea to Easter Island, Pitcairn Island, and Clipperton Island (Emerson & Cernohorsky, 1973).

Genus *Haustrum* Perry, 1811
(Fig. 11A–D)

Haustrum Perry, 1811, pl. 44.
Lepsia Hutton, 1884: 222 [type: *Buccinum haustrum* Martyn, 1784 [non-binomial], by subsequent designation, D. H. Graham, 1941: 155, = *Haustrum haustorium* (Gmelin, 1791)].

Type Species: Haustrum zealandicum Perry, 1811, by subsequent designation, Iredale, 1915: 474, = *Haustrum haustorium* (Gmelin, 1791); synonyms: *Buccinum haustrum* Martyn, 1784 (non-binominal); *Buccinum haustorium* Gmelin, 1791.

Remarks: Haustrum haustrum is a rejected name (ICZN, Opinion 479, 1957: 407), because it was published in a non-binominal work. Thiele (1929: 296) and Wenz (1941: 1117) both recognized *Haustrum* as a genus.

Shell: Protoconch not seen, but reported as having ". . . about 2 smooth whorls, . . ." (Suter, 1913: 422). Teleoconch (Fig. 11A, B) light, ovate, of 5–7 whorls, and with impressed suture, low spire, and high whorl expansion rate. Adult shell about 65 mm in height, 45 mm in width. Body whorl dome-shaped, about 85% of shell height, smooth, with 40–50 incised fine, spiral lines. Aperture very large, about 80% of shell height; apertural lip thin, without denticles, but showing grooved pattern at edge of lip. Columella flattened to concave, with heavy callus layer and axial fold. Anterior siphonal canal moderately short; posterior siphonal canal absent. Siphonal fasciole slightly curved, covered with callus. Shell brown grey, grooves white; columella white, with brown smudge on upper region; aperture white, with thin brown rim on edge.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (45–50%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–7%); calcitic layer (15–20%) (Fig. 11C).

Operculum: D-shaped, upper end rounded, with lateral nucleus in lower right (compare Fig. 1D). Free surface with staff-shaped growth lines; attached surface with about 1–3 arch-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot and tentacles unpigmented to faint yellowish. Kidney light cream brown. Digestive gland dark green. Cephalic tentacles short and stubby. Mantle edge follows contour of aperture. Incurrent siphon very short, not extending beyond mantle edge. Small accessory boring organ dorsal to wide pedal gland with folds (Fig. 4B).

Osphradial length less than one-half ctenidial length; osphradium and ctenidium equal in width or osphradial width slightly less than ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamella attached along one-half of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae about as wide as deep. Lateral edge of ctenidial lamellae convex; ventral edges concave. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections (more pronounced in posterior lamellae).

Vaginal opening round, with diameter one-half that of capsule gland, situated on end of short tube, and located directly below anal opening. Bursa copulatrix running dorso-ventrally, splitting into capsule gland on right, and blind sac on lower left. Ventral channel minute, present only for short distance beneath ventral and left lobe, then present as few, thin ridges emanating from ventral epithelium; posteriorly, ventral channel formed

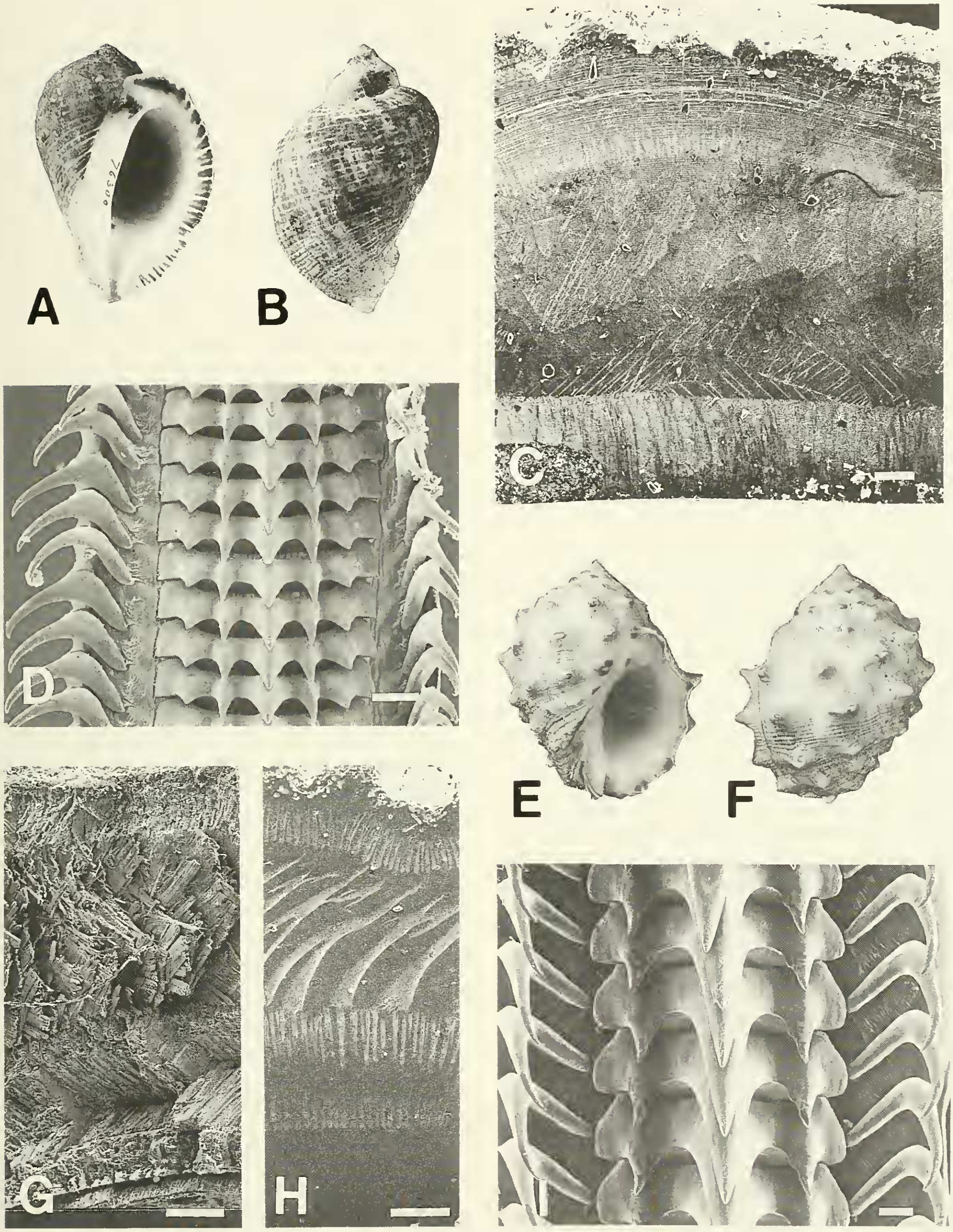

FIG. 11. A–D, *Haustrum haustorium*. A, shell (48 mm), apertural view. B, shell (48 mm), abapertural view. C, shell ultrastructure, SEM (bar = 0.10 mm). D, radula, SEM (bar = 25 μm). E–I, *Mancinella alouina*. E, shell (44 mm), apertural view. F, shell (44 mm), abapertural view. G, shell ultrastructure, SEM (bar = 0.20 mm). H, shell ultrastructure, polished surface, SEM (bar = 0.20 mm). I, radula, SEM (bar = 40 μm).

by flange originating from ventral epithelium, with minute longitudinal ridges (inward projections in cross section). Albumen gland arch-shaped, very elongate. Ovary olive green.

Penis small, lightly curved, smooth, and dorso-ventrally flattened. Penial duct open (perhaps due to poor preservation), very narrow, dorsal and along posterior margin of penis. Cephalic vas deferens closed, visible externally as thin, clear white line directly below surface. Duct continuing posteriorly on interior of mantle as open canal before entering prostate. Prostate small, solid, grey, opaque with dorso-ventral slit, adjacent to rectal wall. Seminal vesicles convoluted, poorly developed, dirty white.

Proboscis large, unpigmented, narrower than gland of Leiblein. Right accessory salivary gland long, thin, nearly one-half of shell height, located in right upper anterior corner of buccal mass, extending posteriorly and ventrally, adjacent to right side of salivary glands. Left accessory salivary gland absent. Yellow salivary gland mass consisting of elongate portions of glandular material with multitude of small threads. Well-developed left part of salivary mass about equal in size to right accessory salivary gland. Valve of Leiblein elongate, partially attached to salivary glands. Salivary ducts attached at varying distances from valve of Leiblein, which lies at least one length away from nerve ring. Portion of mid-esophagus with glandular folds long; folds poorly developed. Well-developed, long duct between esophagus and gland of Leiblein, nearly or about as thick as posterior esophagus. Posterior esophagus attached by minute threads of connective tissue to lower left portion of gland of Leiblein. Gland of Leiblein large, spiral, forming two folds, of hard consistency, light brown, with external strawlike membrane thickest in older specimens. Posterior duct very short (few mm), terminating with ampulla.

Stomach U-shaped, with large posterior mixing area. About 20 distinct folds, oriented towards center, on stomach wall, with minute lines crossing over. Yellow layer overlays grey, opaque folds. Two digestive diverticula present. Intestinal typhlosole well developed, with small, small parallel folds in intestinal groove. Intestine with many small lateral folds of varying sizes. Rectum very large in diameter. Rectal gland undetectable from outside due to dark brown to black hypobranchial gland. Anal opening large, well defined, with upward-pointing anal papilla.

Radula: Ribbon length approximately 20–25% of shell height (Fig. 11D). Short central cusp of rachidian wide at base; elongate, needle-shaped, well-developed, cusplike inner denticles separate from lateral cusps, and nearly as long as central cusp; outer edge of short and wide lateral cusps straight, devoid of denticles, sloping towards rachidian base. Lateral teeth thin, smooth, slightly longer than one-half of rachidian width.

Egg Capsules: Oval to circular, about 6 mm in height, with large, central, ovate exit hole. All capsules attached at common basal membrane (D. H. Graham, 1941).

Ecology: This species lives in the intertidal on rocks (Powell, 1979).

Distribution: New Zealand (Powell, 1979) and southern Australia (W. F. Ponder, personal communication).

Genus *Mancinella* Link, 1807
(Fig. 11E–I)

Mancinella Link, 1807: 115.

Type Species: Mancinella aculeata Link, 1807, by absolute tautonymy through its cited synonym, *Murex mancinella* Linnaeus, 1758 (ICZN, Opinion 911, 1970: 20), = *Mancinella alouina* (Röding, 1798); synonyms: *Mancinella mancinella* (Linnaeus, 1758), *species dubium,* rejected name (ICZN, Opinion 911, 1970: 21); *Volema alouina* Röding, 1798; ?*Volema glacialis* Röding, 1798; *Purpura gemmulata* Lamarck, 1816.

Remarks: Cossmann (1903: 71) placed *Mancinella* in the synonymy of *Purpura* Bruguière. Thiele (1929: 297), Clench (1947: 83), Keen (1971b: 549) and Abbott (1974: 1118) used *Mancinella* as a subgenus of *Thais.* Wenz (1941: 1118) used *Mancinella* as a full genus.

Cernohorsky (1969: 296–297) stated that *Mancinella mancinella* Linnaeus, 1758, is the type of the genus by tautonymy, although the Linnaean taxon is a composite species. Cernohorsky points out that it is clear that Linnaeus only described one of the specimens (*Mancinella mancinella* of authors) in the "*Murex mancinella*" box in the Linnaean collection. However, Vokes (1970) noted that Linnaeus' description does not fit any of the specimens in the box. Vokes followed F. A. Smith (1913: 287) and considered *Murex mancinella* a *nomen dubium.* Keen (1964) petitioned the ICZN that *Mancinella gemmulata*

(Lamarck, 1816) (= *M. aculeata* Link) be designated as the type of *Mancinella*. The ICZN ruled (Opinion 911, 1970: 20) that *Mancinella aculeata* be the type species of the genus *Mancinella*. An available earlier name for *Mancinella aculeata* is Röding's *Volema alouina*.

Shell: Protoconch unknown. Teleoconch (Fig. 11E, F) strong, oval, squat, of about five adpressed whorls. Adult shell up to about 60 mm in height, 40 mm in width. Globose body whorl about 95% of shell height and sculptured with five spiral rows of 9–10 occasionally spinelike, axially arranged knobs. Largest knobs on second and third row, knobs on fifth row weakest. About ten narrow minute ridges between rows. Aperture large, about 75% of shell height. Apertural lip with 10–12 spiral striae beginning about 1 cm from apertural edge. Siphonal canal moderately developed, deep, semi-closed. Columella flat to slightly concave, with angular curve in lower portion forming part of short, open anterior siphonal canal; posterior siphonal canal absent. Siphonal fasciole with 5–6 knobs. Shell cream brown, knobs rusty brown, especially when worn; aperture and columella light to dark orange, with apertural striae dark orange.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (15–20%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (7–9%); calcitic layer (4–6%) (Fig. 11G, H).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 4–7 bracket-shaped growth lines and with callused, glazed rim (about 35–45% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot and tentacles rusty, light to dark brown. Kidney olive green. Hypobranchial gland bright light green. Digestive gland grey brown. Mantle edge smooth; incurrent siphon extending far from mantle edge. Accessory boring organ dorsal to pedal gland (Fig. 4B).

Osphradial length slightly more than one-half ctenidial length; osphradial width nearly equal to ctenidial width. Osphradium symmetrical in shape along lateral axis; right pectin wider than left. Osphradial lamellae attached along very small portion of their base.

Anteriormost portion of ctenidium straight, extending slightly farther anteriorly than osphradium. Anterior and posterior ctenidial lamellae as deep as wide. Lateral edges of ctenidial lamellae faintly S-shaped; ventral edges concave.

Vaginal opening central, slightly protruded on short tubular oviduct and located below and posterior to anal opening. Bursa copulatrix short, as part of vagina and anterior to capsule gland. Ventral channel formed by small flange originating from ventral epithelium. Ventral flange with few longitudinal ridges and located under ventral lobe. Ingesting gland a single chamber (not visible from outside). Albumen gland of the omega- or arch-shaped type, with many long, white seminal receptacles on dorsal periphery. Ovary yellow (in preserved specimens).

Penis strongly recurved, with flagelliform tip, dorso-ventrally flattened. Penial vas deferens as central, minute duct-within-a-duct system occupying about one-sixth of penial width. Cephalic vas deferens thin, running along mantle prior to entering prostate. Prostate small, yellow, with central duct, smaller in diameter than adjacent rectum.

Proboscis large, unpigmented, nearly equal in width to gland of Leiblein. Paired accessory salivary glands very small, short, thin; left gland located in left anterior portion of buccal mass adjacent to salivary gland mass; right accessory salivary gland located in right anterior portion of buccal mass, adjacent to proboscis. Salivary glands small, yellowish, located to left of proboscis, and anterior to gland of Leiblein. Salivary ducts attached to anterior portion of esophagus directly anterior of valve of Leiblein. Valve of Leiblein elongate, adjacent to nerve ring. Folds on mid-esophagus nearly indiscernible. Duct between mid-esophagus and gland of Leiblein short and much thinner than posterior esophagus. Posterior esophagus adjacent to lower left portion of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, yellowish, with thin external membrane. Posterior duct about one-half of length of gland of Leiblein and with terminal ampulla.

Stomach nearly rectangular, with large posterior mixing area. About 12–15 folds on stomach wall, oriented towards center of stomach. Two digestive diverticula present. Stomach typhlosole only moderately developed. Intestinal typhlosole thin. Intestinal wall with many minute lateral lines and small folds. Intestinal groove with few thin longitudinal folds. Rectum with moderate diameter. Anal opening well defined, with anal papilla.

Radula: Ribbon length about 25% of shell height (Fig. 11I). Rachidian with thick, needle-shaped central cusp; short, wide lateral cusps smooth, with outside edge sloping to rachidian edge. Lateral teeth smooth, about three-fourths of rachidian width.

Egg Capsules: Unknown.

Ecology: Mancinella alouina lives from the intertidal to subtidal zones on sheltered rocks, whereas *Mancinella echinulata* occurs in crevices on exposed reefs (Kilburn & Rippey, 1982). Remains of small crustaceans were present in the rectum of several animals examined.

Distribution: Red Sea and throughout Indo-Pacific (Cernohorsky, 1969).

Genus *Morula* Schumacher, 1817
(Fig. 12A–G)

Morula Schumacher, 1817: 68, 227.

Tenguella Arakawa, 1965: 123 [type: *Purpura granulata* Duclos, 1832, by original designation, = *Morula granulata* (Duclos, 1832)].

Type Species: Morula papillosa Schumacher, 1817 (*non* Philippi, 1849), by monotypy, = *Morula uva* (Röding, 1798); synonyms: *Drupa uva* Röding, 1798; *Ricinula nodus* Lamarck, 1816; *Ricinula aspera* Lamarck, 1816; *Ricinula morus* Lamarck, 1822; *Purpura sphaeridia* Duclos, 1832; *Ricinula alba* Mörch, 1852; ?*Sistrum striatum* Pease, 1868; ?*Morula nodilifera* Habe & Kosuge, 1966.

Remarks: Thiele (1929: 295) and Wenz (1941: 1114) considered *Morula* a section of the subgenus *Drupa* in the genus *Drupa*. *Morula granulata* was designated as type species of *Tenguella* Arakawa, 1965, based on radular characters (presence and number of marginal denticles). However, the number of marginal denticles is variable in both species and overlap occurs. *Tenguella* is herein considered synonymous with *Morula*.

Shell: Protoconch (Fig. 12C, D) tall, conical, of at least 4.25 adpressed whorls [exact count could not be made from available specimen], sculptured with 3 spiral cords of small bead-like pustules directly below suture, but otherwise smooth, and with outward-flaring lip; sinusigeral notch covered by teleoconch. Teleoconch (Fig. 12A, B) ovate, of 5–6 adpressed whorls, with moderately high spire. Adult shell up to about 27 mm in height, 17 mm in width. Body whorl about 80% of shell height, sculptured with five spiral rows of 12 short but well-developed knobs. One spiral, faintly lamellose ridge between rows with deep groove on each side. Elongate aperture about 68% of shell height. Apertural opening narrow, due to pair of heavy denticles pointing inward. Two smaller denticles located on lower end. Anterior siphonal canal very short, semi-closed; posterior siphonal canal absent. Columella concave; lower part with several faint denticles. Siphonal fasciole strongly curved, previous edges still visible, not knob-like. Shell white, knobs black; aperture and columella pink to violet purple.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (15–25%); aragonitic layer with crystal planes oriented parallel to growing edge (75–85%) (Fig. 12F).

Operculum: D-shaped, with S-shaped left edge, tapered at lower end, with lateral nucleus in lower right (Fig. 1F). Free surface with bracket-shaped growth lines; attached surface with about 4–6 bracket-shaped growth lines and with callused, dull rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals): Head with long cephalic tentacles emanating from common base. Lower part of head-foot mottled black and white to uniform black on lower portion; upper part with white and orange flecks. Tentacles uniform black at bases, white distally, or white with small black lateral band at eye levels. Mantle edge crenate, folded; underside of mantle with black and white patches. Incurrent siphon uniform black, or with white flecks. Kidney caramel brown. Digestive gland dark brown. Sole white with central, opaque, white speckled band, oriented antero-posteriorly. Accessory boring organ large, with short duct opening close to anteriorly located pedal groove. Hypobranchial gland very large, divided into red brown, white, and green portions, and with black rods of unknown composition pointing towards mantle cavity. Ventral pedal gland combined with accessory boring organ.

Osphradial length slightly greater than one-half ctenidial length (Fig. 3D); osphradial

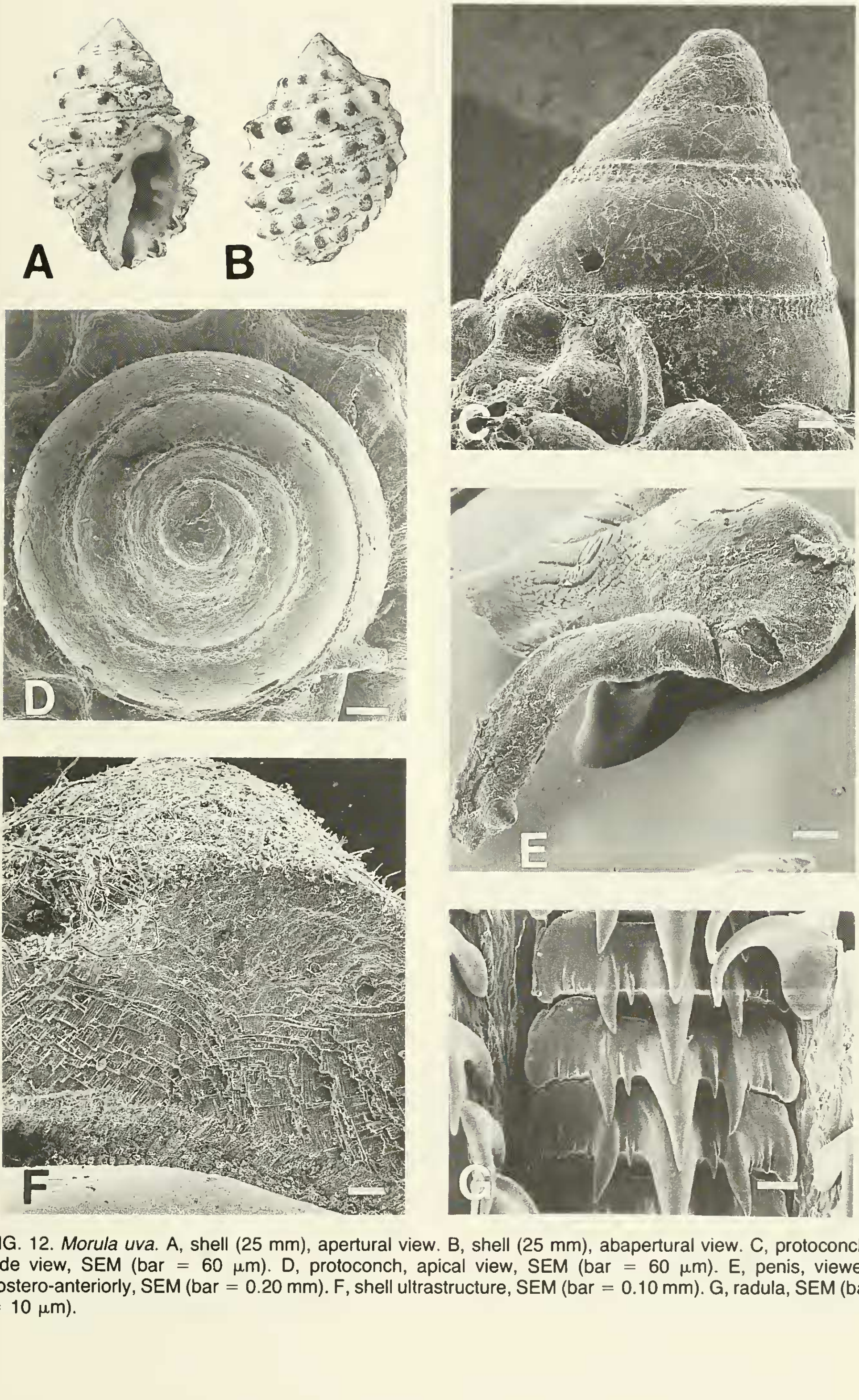

FIG. 12. *Morula uva.* A, shell (25 mm), apertural view. B, shell (25 mm), abapertural view. C, protoconch, side view, SEM (bar = 60 μm). D, protoconch, apical view, SEM (bar = 60 μm). E, penis, viewed postero-anteriorly, SEM (bar = 0.20 mm). F, shell ultrastructure, SEM (bar = 0.10 mm). G, radula, SEM (bar = 10 μm).

width equal to or slightly greater than ctenidial width. Osphradium more tapered at posterior end; right pectin slightly wider than left. Osphradial lamellae attached along most of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae deeper than wide; posterior lamellae as deep as wide. Lateral edges (Fig. 3D, le) of ctenidial lamellae concave; ventral edges straight. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening a short slit (more rounded in juveniles) situated on distal end of tubular extension of pallial gonoduct and located beneath anal opening. Bursa copulatrix as dorso-ventral slit open to vagina and continuous with capsule gland. Vagina continuing as ventral channel with large, circular ventral flange with many longitudinal and well-developed ridges; flange positioned below left lobe of capsule gland anteriorly, smaller, flattened, and below both lobes posteriorly. Ventral channel branching away from capsule gland, forming large posterior bursa. Branch of bursa continuing as oviduct, larger portion as blind sac. Bursa connected to single-chambered ingesting gland with short duct. Ingesting gland larger than albumen gland and black when viewed from outside. Albumen gland staff-shaped, with anterior portion being much shorter and less developed. Few seminal receptacles (3–5) at dorsal side branching from ovi-sperm duct prior to it connecting to albumen gland. Ovary white to yellow. [The female reproductive system of *Morula granulata* was described in detail by Srilakshmi (1991)].

Penis (Fig. 5E, 12E) very large, strongly recurved, round in cross section, V-shaped, with flattened, large side lobe; distal end of penis varying in length and attached by small connection to proximal part of penis. Penial vas deferens as duct-within-a-duct system occupying about one-fifth of penial width. Cephalic vas deferens minute, describing "Z" pattern. Prostate solid, glandular, opaque, white opaque or dark brown, with closed duct; prostate much larger than rectum and not separated from it by layer of epithelium. Seminal vesicles well developed, white to dark orange brown.

Proboscis large, equal in width to gland of Leiblein, occasionally folded and horseshoe-shaped, laying against left side of gland of Leiblein. Paired accessory salivary glands club-shaped, small, equal in length, much smaller than one-half of shell height; left accessory salivary gland embedded in left salivary gland; right gland separate. Salivary glands very large, much larger than accessory salivary glands and almost as large as gland of Leiblein, located dorsally either as separate lobes or solid mass. Salivary ducts attached close to valve of Leiblein. Valve of Leiblein short, with caplike structure on anterior end, and lying adjacent to nerve ring, separate from salivary glands. Glandular folds of mid-esophagus nearly indiscernible. Duct between mid-esophagus and gland of Leiblein very thin. Posterior esophagus separate from gland of Leiblein. Gland of Leiblein spiral, forming two folds, of soft consistency, consisting of small cavities, dark brown, lacking strawlike membrane.

Stomach as wide tube with few very large folds and many minute folds on stomach wall of posterior mixing area. Small unciliated area between posterior mixing area and intestine. Stomach and intestinal typhlosoles very well developed. One diverticulum present directly anterior to esophagus. Anal opening inconspicuous but with very large papilla. Thin rectal gland along entire capsule gland.

Radula: Ribbon length about 15% of shell height (Fig. 12G). Central cusp on rachidian tooth needle-shaped, with moderately wide base; lateral denticle separate from lateral cusp; outer and inner edge of lateral cusp straight, smooth; several stubby marginal denticles present on wide, horizontal edge of rachidian; wide, short marginal cusp. Lateral teeth strongly curved, smooth, with wide base; about one-half of rachidian width.

Egg Capsules: Unknown.

Ecology: Common on intertidal limestone benches, where it feeds almost exclusively on vermetid gastropods (Kay, 1971; Miller, 1970; J. D. Taylor, 1976, 1984).

Distribution: Indo-Pacific, from Red Sea to Isla Guadalupe and Clipperton Island (Cernohorsky, 1969; Keen, 1971b).

Genus *Nassa* Röding, 1798
(Fig. 13A–G)

Nassa Röding, 1798: 132 (*non* Lamarck, 1799, = *Nassarius* Duméril, 1806).

Iopas H. & A. Adams, 1853: 128 [type: *Buccinum sertum* Bruguière, 1789, by sub-

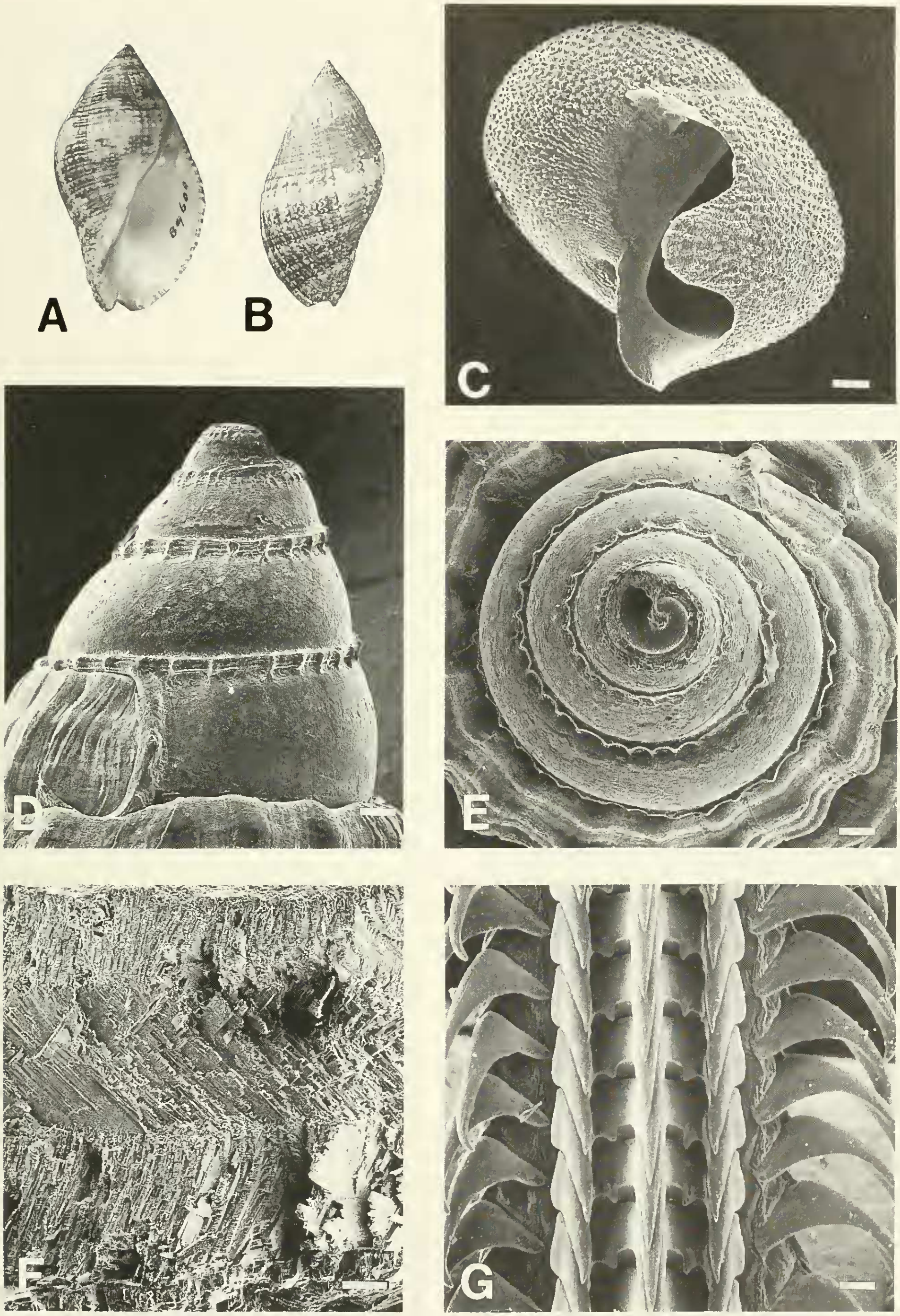

FIG. 13. A–C, F–G, *Nassa serta:* A, shell (40 mm), apertural view. B, shell (44 mm), abapertural view. C, larval shell, side view, SEM (bar = 25 μm). F, shell ultrastructure, SEM (bar = 0.10 mm). G, radula, SEM, (bar = 25 μm). D–E, *Nassa* "*francolina*" D, protoconch, side view, SEM (bar = 80 μm). E, protoconch, apical view, SEM (bar = 80 μm).

sequent designation, Baker, 1895: 185, = *Nassa serta* (Bruguière, 1789)].
Jopus Schaufuss, 1869 (error for *Iopas*).
Jopas Baker, 1895: 185 (unjustified emendation of *Iopas*).

Type Species: According to a number of authors (Winckworth, 1945; Iredale & McMichael, 1962; Cernohorsky, 1969), Dall (1909) subsequently designated *Nassa picta* Röding, 1798, as the type species of *Nassa*. However, Dall (p. 47) does not list the name *picta,* but rather "*Purpura sertum* Lam" as type of *Nassa,* which was not one of the species included by Röding and is therefore unavailable. I can find no valid subsequent designation and here designate the type species as *Nassa picta* Röding, 1798, = *Nassa serta* (Bruguière, 1789); synonyms: *Buccinum sertum* Bruguière, 1789; *Buccinum coronatum* Gmelin, 1791; ?*Stramonita hederacea* Schumacher, 1817; ?*Buccinum francolinus* Bruguière, 1789; *Buccinum situla* Reeve, 1846.

Remarks: Cossmann (1903: 68) considered *Nassa* a full genus (as *Iopas*), and included, besides *Iopas s.s, Taurasia* Bellardi, 1882. Thiele (1929: 296) used *Jopas* and included the subgenera *Jopas* (= *Nassa*) and *Vexilla*. Wenz (1941: 1116) used *Nassa* and included the subgenera *Nassa, Vexilla,* and *Taurasia*.

Controversy exists about whether the genus *Nassa* contains one or two species. The nominal species *serta* and *francolina* can be separated on the basis of shell sculpture and geographic distribution (see "Distribution"). Individuals from the Pacific Ocean, traditionally grouped under *N. serta,* have shells with relatively coarse spiral ribs, whereas the shells of Indian Ocean specimens have very fine spiral lines and appear nearly smooth. I suspect, however, that future research will show that these taxa are conspecific, considering the range of variation in sculptural patterns in many other rapanine species.

Shell: Embryonic shell (Fig. 13C) with well-developed beak and pattern of spiral rows of microscopic volcanolike pustules. Protoconch (Fig. 13D, E; typical *N. francolina*) tall, conical, of at least 4.25 adpressed whorls [exact count could not be made from available specimen], with subsutural plicae interconnected by three thin spiral ridges, but otherwise smooth, and with outward-flaring lip; sinusigeral notch covered by teleoconch. Teleoconch (Fig. 13A, B) elongate, slender, fusiform, of 6–7 adpressed whorls. Adult shell up to about 70 mm in height, 35 mm in width. Body whorl rounded, about 85–90% of shell height. Body whorl sculptured with about 30 small, spiral cords of minute pustules, nearly smooth in typical *N. francolina.* Aperture elongate, large, about 75% of shell height, curved angularly at base to form part of siphonal canal. Apertural lip smooth interiorly, but crenate at edge, corresponding to external pattern of small ridges. Siphonal notch wide and open. Columella lightly callused and rounded. Posterior siphonal canal absent, but protrusion of columellar callus directly across from similar protrusion on inside of apertural lip forming canal in posteriormost end of aperture. Siphonal ridge with similar pattern as on body whorl, slightly curved, adjacent to columellar callus. Shell with varying color patterns comprising combinations of cream (usually as median band running around body whorl), light and dark brown spiral bands which may consist of blotches; aperture white with some yellow tinges towards edge, and dark brown crenulations on edge, corresponding with dark brown spiral ridges; top of columella yellow white, caramel brown at base.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (45–50%); aragonitic layer with crystal planes oriented parallel to growing edge (30–35%); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–20%) (Fig. 13F).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface without distinct growth lines and with callused, glazed rim (about 45–55% of opercular width) on left.

Anatomy (based on living and preserved animals): Cephalic tentacles long, uniform black, with distal halves of tips white. Head-foot uniform black, lightly spotted with white. Mantle edge simple and straight. Incurrent siphon long, uniform black. Hypobranchial gland brown to yellow. Kidney brown. Nephridial gland S-shaped, wide, opaque. Digestive gland dark brown. Sole of foot yellow, with pattern of thin ridges. Accessory boring organ with long duct. Pedal gland large, located under accessory boring organ (Fig. 4B).

Osphradial length equal to or greater than ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae of right pectin attached along one-half of their base; those of left pectin attached along entire base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae much deeper than wide. Lateral and ventral edges of ctenidial lamellae variable in shape. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening slit-shaped, with two longitudinal flanges in opening and located below and posterior to anal opening. Bursa copulatrix as large storage area with fine horizontal lines, continuous with capsule gland. Small, circular flange originating from ventral epithelium, under small ventral lobe of anterior portion of capsule gland; flange minute, hooklike posteriorly, perpendicular to capsule gland lobes. Flange split at base in central portion of capsule gland. Ingesting gland as large thin-walled chamber containing granular, caramel brown material. Seminal receptacles on dorsal periphery of omega-shaped albumen gland elongate to club-shaped, white, nearly reaching oviduct. Ovary orange.

Penis long, thin, slightly recurved, flagelliform, oval in cross section (Fig. 5C). Penial vas deferens as duct-within-a-duct system occupying one-fourth of penial width. Cephalic vas deferens thin, inconspicuous. Prostate small, white, with central duct, separated from very large rectum by epithelial layer. Seminal vesicles well developed, white.

Proboscis very large, equal in width to gland of Leiblein, white. Paired accessory salivary glands thin, equally long, about one-third of shell height. Left accessory gland adjacent to salivary gland mass; right gland in anterior right area of buccal cavity separate from salivary gland mass. Paired accessory salivary glands equal in size to salivary gland mass. Salivary glands inseparable, oriented dorso-ventrally. Valve of Leiblein elongate, not embedded in salivary glands. Salivary ducts attached to anterior portion of valve of Leiblein. Valve of Leiblein adjacent to nerve ring. Portion of mid-esophagus with glandular folds short, well developed. Duct between mid-esophagus and gland of Leiblein distinct, but thinner than esophagus. Posterior esophagus attached to lower left portion of gland of Leiblein. Gland of Leiblein spiral, forming one fold, light brown, with strawlike membrane. Posterior blind duct of gland of Leiblein longer than one-half of length of gland itself and opening into dorsal branch of renal afferent vein, extending beyond kidney opening.

Stomach as wide tube with large posterior mixing area. Large number of folds on stomach wall of posterior mixing area; folds oriented towards stomach center; each one containing many lateral folds, directing small particles laterally. Stomach typhlosole well developed with two digestive diverticula at base; intestinal typhlosole narrow but distinct. Several small elongate folds in intestinal groove. Large bulbous papilla extending from dorsal rectal wall, lying over very small anal opening. Large thick orange gland over pallial gonoduct. Rectal gland dark green, thin, along entire capsule or prostate.

Radula: Ribbon length about 25% of shell height (Fig. 13G). Rachidian with thin central cusp; inner lateral cusp denticle separate from lateral cusp in males; denticle may be absent, especially in narrower rachidian tooth of females (see Maes, 1966); lateral cusps smooth, less developed in female specimens relative to central cusp; outer edge of lateral cusps sloping nearly straight down to edge of rachidian. Lateral teeth very wide at base and as long as rachidian width.

Egg Capsules: Cylindrical, 6–8 mm in height; base wide, 1–2 mm in length. Some appearing to consist of four sides, base constricted lengthwise along axes. All capsules attached to basal membrane. Exit hole on circular apical plate, usually slightly off center.

Ecology: Nassa serta lives under boulders and coral rubble on limestone benches and reef flats of the Pacific Ocean. Analysis of stomach contents revealed rachidian teeth of *Nassa* radula, suggesting cannibalism. Some specimens were found laying egg capsules under a large piece of coral rubble at low tide.

Distribution: Indian Ocean, from Cocos-Keeling Islands (Maes, 1967: 132) throughout tropical Pacific Ocean (Abbott & Dance, 1982) (typical *Nassa serta*); in remainder of Indian Ocean (Cernohorsky, 1969) usually referred to as *Nassa francolina*.

Genus *Neorapana* Cooke, 1918
(Fig. 14A–F)

Neorapana Cooke, 1918: 7 (as a subgenus of *Acanthina* Fischer von Waldheim, 1807).

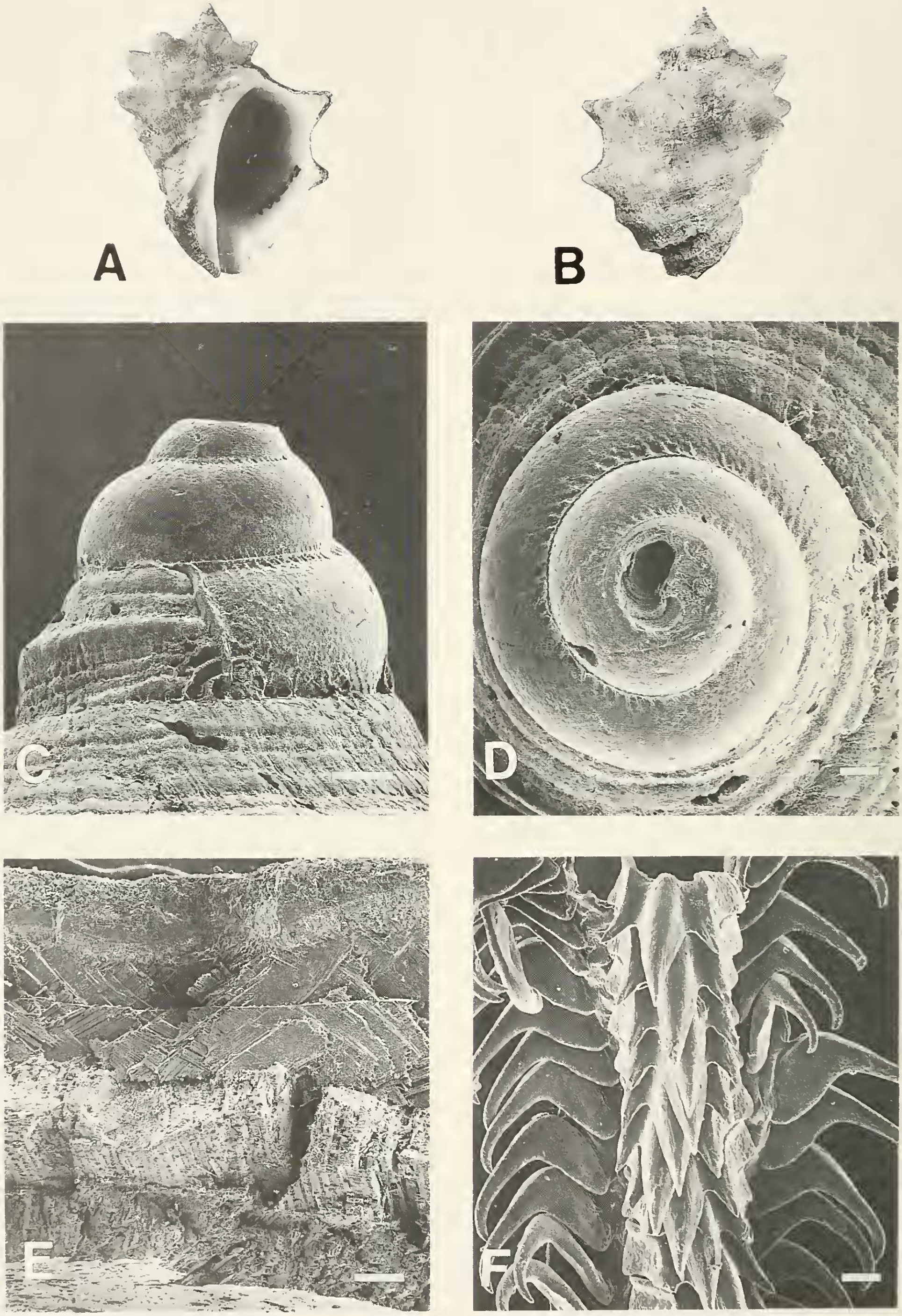

FIG. 14. *Neorapana muricata.* A, shell (45 mm), apertural view. B, shell (45 mm), abapertural view. C, protoconch, side view, SEM, (bar = 0.20 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, SEM (bar = 0.20 mm). F, radula, SEM (bar = 35 μm).

Type Species: Purpura muricata Broderip, 1832, by original designation, = *Neorapana muricata* [Broderip, 1832]; synonyms: *Purpura truncata* Duclos, 1832; *Monoceros tuberculatum* Sowerby, 1835, *ex* Gray Ms.

Remarks: Cooke based his separation of *Neorapana* from *Acanthina s.s.* on radular characters. The shell of *N. muricata* resembles that of species of *Acanthina* in having a labial tooth. This single character was the primary criterion for inclusion of this species in the genus *Acanthina* by several authors. Thiele (1929: 297) allotted *Neorapana* section status under the subgenus *Mancinella* of the genus *Thais*. Wenz (1941: 1118) considered *Neorapana* a subgenus of *Thais*. Keen (1971b: 554) considered *Neorapana* a full genus in the Rapaninae.

Specimens of *Neorapana muricata* used in this study are representatives of typical *Neorapana tuberculata* (Sowerby, 1835); *N. muricata* has a greater distribution, ranging from Guaymas, Mexico, to Ecuador, whereas typical *N. tuberculata* ranges from Cabo San Lucas, Mexico, throughout the Gulf of California to Mazatlán, Mexico (Keen, 1971b), thus partially overlapping in range with *N. muricata.* I regard the latter as merely a form or variant of the former; intergrading shell forms suggest conspecificity. Detailed anatomical and molecular studies, however, could show these forms to be different species. But until such a study has been performed, I will continue considering these two names to be synonyms, with *muricata* having priority over *tuberculata.*

Shell: Protoconch (Fig. 14C, D) tall, conical, of at least 3.25 adpressed whorls [exact count could not be made from available specimen], with faint, small subsutural plicae and microscopic pustules (last whorl), and with outward-flaring lip; sinusigeral notch covered by teleoconch. Because the descriptions of *N. muricata* beyond the shell morphology are based on "tuberculate" specimens, a description of the tuberculate shell morph follows. Teleoconch (Fig. 13A, B) large, heavy, conical, of 5–6 adpressed whorls. Adult up to about 60 mm (80 mm in typical *N. muricata*) in height, 45 mm (70 mm in typical *N. muricata*) in width. Body whorl about 85–90% of shell height, somewhat dome-shaped, sculptured with well-developed shoulder, and bearing four rows of spiral bands of 6–7 knobs. Suture lying adjacent to and following lower contours of second row of knobs on penultimate whorl. First row of knobs on angular shoulder, highly developed and with discontinuous ridge on knobs. Second, third and fourth rows consecutively less developed. Knobs of two uppermost rows lying directly under and above each other, as do third and fourth row, but knobs on latter pair not axially aligned with knobs on first two rows. Five to eight narrow, delicately lamellose spiral ridges between pairs of rows of knobs. Aperture large, about 80–90% of shell height. Apertural lip with 12–16 ridges on inside surface, most pronounced on last growth increment. Edge of lip crenate and thin. Anterior siphonal canal short, well developed in some specimens, but only a notch in others; posterior siphonal canal poorly developed. Columella lightly to heavily callused, rounded to concave. Siphonal fasciole strongly curved, bending outward and free of callus margin. Shell cream to yellow orange brown; columella white to yellow; interior apertural lip white to yellow orange.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45°-angle to growing edge (15–20%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–8%); calcitic layer (8–15%) (Fig. 14E).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 3–6 bracket-shaped growth lines and with callused, glazed rim (about 45–50% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot mottled black on white base. Mantle edge crenate, following aperture contour. Siphon long, black and white, extending some distance beyond mantle edge. Hypobranchial gland with cottonlike appearance. Digesting gland caramel brown (one male examined) or dark olive green (one female examined). Accessory boring organ relatively small, dorsal to narrow ventral pedal gland in females (Fig. 4B), with small transverse folds on transition zone.

Osphradial length about one-half ctenidial length; osphradial width less than one-half ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae wider than deep. Lateral edge of ctenidial lamellae strongly concave; ventral edge moderately concave or S-shaped. Distal tips of ctenidial support rods extending beyond lateral edge as papillate projections.

Vaginal opening slit-shaped, situated on distal end of short, attached, tubular extension of pallial gonoduct, and located below and slightly posterior to anus. Bursa copulatrix small, with large inner ridges; bursa in open connection with vagina and located on right side of it, continuous with capsule gland. Large, complex ventral flange located under right lobe of capsule gland. Ingesting gland very large, dark brown, filled with dark brown granular chunks; single chambered, with small tubes connecting walls; extending from dorsal left posterior portion of capsule gland to left of albumen gland. Albumen gland omega-shaped, tilted strongly backwards. Seminal receptacles on dorsal periphery of albumen gland white.

Penis strongly recurved, elongate, thick, muscular gradually tapering, and oval in cross section. Penial vas deferens as minute duct-within-a-duct system occupying one-eighth of penial width. Prostate white, with large longitudinal central opening closed, directly adjacent to rectum. Seminal vesicles well developed, orange or white.

Proboscis black and white, much thinner than gland of Leiblein. Paired accessory salivary glands thin, equally long, about one-third of shell height; left gland adjacent to salivary gland, right one largely separate from salivary gland. Paired salivary glands as joined mass, each lobe consisting of many worm-shaped strands connected by small ducts. Valve of Leiblein elongate, separate from salivary gland mass, a considerable distance from nerve ring. Salivary ducts attached to anterior portion of esophagus directly anterior of valve of Leiblein. Glandular folds on mid-esophagus inconspicuous. Duct between gland of Leiblein and esophagus poorly developed. Posterior esophagus attached to posterior lower left side of gland of Leiblein. Gland of Leiblein large, spiral, forming one fold with hole in center for passage of anterior aorta, of hard consistency, yellow to cream, and with thin strawlike membrane. Posterior blind duct of gland of Leiblein about one-half of length of gland of Leiblein and entering dorsal branch of afferent renal vein.

Stomach tubular, with large posterior mixing area, with 6–15 folds on stomach wall oriented towards center of stomach. Stomach typhlosole very large, sometimes continuing up left portion of stomach wall. Intestinal typhlosole thin, flat. Several small folds in intestinal groove. Wide, thick fold demarcating entrance of intestine in older female specimens. Smooth area adjacent to thick fold. Two large digestive diverticula present. Rectum of moderate diameter, embedded in spongy connective tissue. Long papilla lying over distinct but small anal opening. Wide rectal gland adjacent to most of prostate and capsule gland.

Radula: Rachidian with thick, wide central cusp, nearly one-third of rachidian width (Fig. 14F); inner edge of lateral cusps convex, outer edge slightly concave; outer edge of lateral cusp sloping steeply towards marginal edge of rachidian, and with faint minute folds on lower base. Lateral teeth with wide bases and curving "hooked" tips; length of lateral teeth greater than rachidian width.

Egg Capsules: Unknown.

Ecology: Neorapana muricata lives on boulders in the intertidal zone but may occur in the sublittoral. I found many specimens partially buried in sand at the sand-rock interface; it is not clear whether this resulted from burrowing behavior or from sediment accumulation. Small crabs were present in the mantle of two specimens of *Neorapana muricata*. The diet of this species is not known.

Distribution: Eastern Pacific, from eastern Baja California, Mexico, to Ecuador (Keen, 1971b).

Genus *Nucella* Röding, 1798
(Fig. 15A–G)

Nucella Röding, 1798: 130.

Polytropa Swainson, 1840: 80, 305 [type: *Buccinum lapillus* Linnaeus, 1758, by subsequent designation, Gray, 1847: 138, = *Nucella lapillus* (Linnaeus, 1758)].

Polytropalicus Rovereto, 1899: 105 (unnecessary replacement name for *Polytropa* Swainson; section of *Purpura*) (*nomen dubium*).

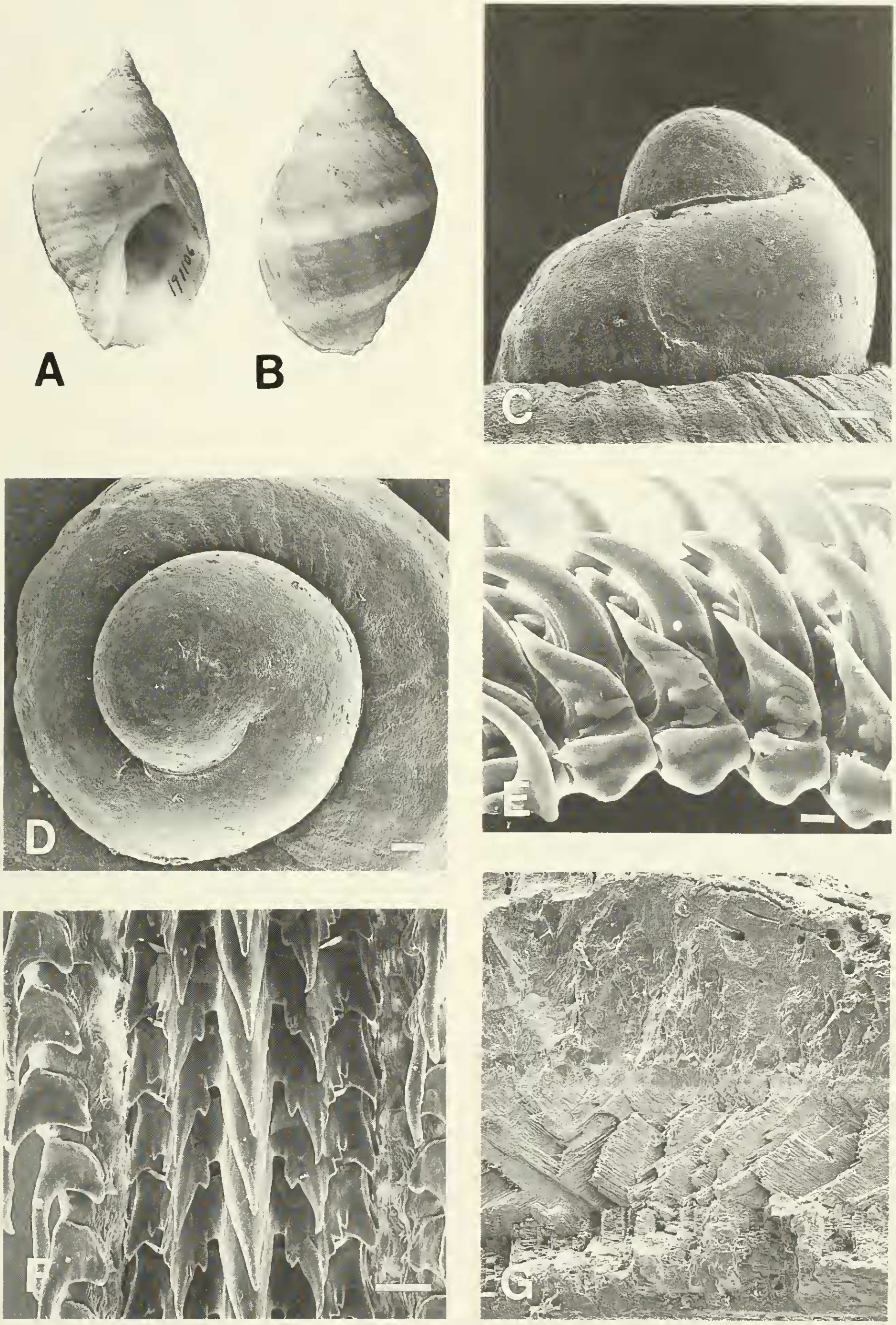

FIG. 15. *Nucella lapillus.* A, shell (32 mm), apertural view. B, shell (32 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, SEM (×55). F, radula, SEM (bar = 20 μm). G, radula, side view, SEM (bar = 10 μm).

Type Species: Buccinum filosum Gmelin, 1791, by subsequent designation, Stewart, 1927: 386 (footnote 260), = *Nucella lapillus* (Linnaeus, 1758); synonyms: *Buccinum lapillus* Linnaeus, 1758: 739; *Nucella theobroma* Röding, 1798; *Purpura imbricata* Lamarck, 1822; *Purpura bizonalis* Lamarck, 1822; *Purpura buccinoidea* Blainville, 1829; *Purpura celtica* Locard, 1886; *Coralliophila rolani* Bogi & Nofroni, 1984.

Remarks: Cossmann (1903: 68) recognized Rovereto's subgenus *Polytropalicus,* not realizing that it was an unnecessary replacement name for *Polytropa.* Thiele (1929: 298) included the sections *Nucella, Acanthina, Acanthinucella* Cooke, 1918, and *Neothias* (as *Neothais;* unjustified emendation) in the genus *Nucella.* Wenz (1941: 1123) raised these sections to subgeneric status under *Nucella. Nucella* species have often been placed in *Thais* and *Purpura.* For detailed information on the taxonomic history of the type species designation for *Nucella,* see Rehder (1962) and Kool & Boss (1992).

Shell: Protoconch (Fig. 15C, D) short, conical, of about 1.25 smooth whorls, and with impressed suture; transition with teleoconch smooth. Teleoconch (Fig. 15A, B) highly polymorphic, but usually elongate, oval, of 6–7 adpressed whorls. Adult shell up to about 55 mm in height, 30 mm in width. Body whorl rounded, about 80% of shell height, smooth or sculptured with pattern of 15 spiral, occasionally lamellose ridges. Aperture oval, about 65% of shell height; apertural lip wide, inside smooth, occasionally with 3–4 denticles on edge of thickened lip. Anterior siphonal canal short, open or semi-closed; posterior siphonal canal absent. Columella with moderate amount of callus, flat to concave, with angular curve in lower portion to form part of siphonal canal. Siphonal fasciole poorly developed, adjacent to callus layer. Shell color variable: white, grey, yellow, brown, orange-red; often with banding patterns of these colors; aperture and columella white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (15–25%) (not always present); aragonitic layer with crystal planes oriented parallel to growing edge, occasionally colored reddish brown (15–35%); calcitic layer (40–85%) (Fig. 15G).

Operculum: D-shaped, upper end rounded, with lateral nucleus in lower right (compare Fig. 1D). Free surface with staff-shaped growth lines; attached surface with about 3–5 arch-shaped growth lines and with callused, glazed rim (about 35–40% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot light yellow to white, with elongate, thin cephalic tentacles and short anterior siphon. Mantle edge smooth, straight. Sole of foot with ridges. Small nephridial gland arching over pericardium. Large accessory boring organ separated from adjacent, equally large pedal gland present in females (Fig. 4A).

Osphradial length slightly more than one-third ctenidial length; osphradial width less than one-half ctenidial width. Osphradium symmetrical in shape along lateral axis; right pectin usually wider than left. Osphradial lamellae attached along one-half of their base.

Anteriormost portion of ctenidium straight, extending slightly farther anteriorly than osphradium. Anterior ctenidial lamellae wider than deep or as wide as deep; posterior lamellae as wide as deep. Lateral edge of ctenidial lamellae varying from strongly convex to straight; ventral edge straight. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening round with slightly swollen surrounding edges and located below and posterior to anus. Bursa copulatrix a large diverticulum, connected to vagina by wide ventral passage. Ventral channel formed by two small interlocking flanges located under ventral lobe of capsule gland, one arising from left lobe, the other from ventral epithelium. Albumen gland arch-shaped, elongate. Single-chambered ingesting gland extending between capsule gland and albumen gland. Ovary yellow to light golden in living specimens. Pseudo-penis usually present in females.

Penis dorso-ventrally flattened, straight or lightly curved, and with abruptly tapering, papillalike end. Penial vas deferens as minute, simple duct, semi-closed by overlapping ventral and dorsal sides of penis. Cephalic vas deferens well developed. Prostate gland bilobed, white, with dorso-ventral slit partially open to mantle cavity. Vas deferens poorly developed, whitish, separated from rectum by epithelial layer. Testis light brown to golden in living specimens.

Paired accessory salivary glands extremely long, usually longer than one-half of shell height; left gland intertwined with salivary gland mass, right one separate from salivary gland mass and located in right anterior corner of buccal cavity. Salivary gland mass in center of dorsal buccal cavity between gland of Leiblein and short, pear-shaped valve of Leiblein. Salivary ducts attached to anterior portion of esophagus at some distance from valve of Leiblein. Glandular folds on mid-esophagus indiscernible. Duct between mid-esophagus and gland of Leiblein short, thick. Esophagus attached to left side of gland of Leiblein in horseshoe-shape. Gland of Leiblein spiral, of hard consistency, yellowish. Posterior blind duct very short, with terminal ampulla.

Stomach tubular, with 8–12 large folds on stomach wall oriented toward center of stomach. Stomach typhlosole extending upwards on left portion of posterior mixing area. Intestinal typhlosole thick, wide. Two digestive diverticula present. Large papilla lying over equally large anal opening. Rectal gland sometimes not apparent.

Radula: About 30–35% of shell height (Fig. 15E, F). Rachidian widening dramatically from cusp bases toward base of rachidian; central cusp of rachidian thin, somewhat constricted at base; inner lateral denticle low on base of lateral cusp, and occasionally bifurcate; straight outer edge of lateral cusp with several short denticles at base; base of lateral cusp adjacent to base of large marginal cusp; marginal cusps in different plane than lateral cusps (about 75° angle) and parallel to elongate lateral extension at base of rachidian tooth, resulting in bifid rachidian edge. Lateral teeth shorter than rachidian width.

Egg Capsules: Oval-elongate, vase-shaped, up to about 9 mm in height, 3 mm in width, each attached with short, thin base about 1 mm long. Apex tapered with central exit hole. Capsules deposited some distance from other capsules but interconnected by base. Each capsule contains up to 600 embryos, 94% of them being nurse eggs (Crothers, 1985).

Ecology: Probably more is known about *Nucella* ecology than that of any other muricid. *Nucella lapillus* and its western American congeners have been the topic of many comprehensive studies (Kincaid, 1957; Crothers, 1985) and Ph.D. dissertations (Emlen, 1966; Spight, 1972; Etter, 1987). *Nucella* feeds on barnacles and mussels (Largen, 1967; Murdoch, 1969; Connell, 1970; Crothers, 1973; Spight, 1982) in the rocky intertidal zone and is eaten by crabs and birds (Spight, 1976). Moore (1938) reported winter and spring to be the main spawning period.

Studies show that environmental factors (wave action, food availability, etc.) drastically influence shell morphology (Cooke, 1895; Agersborg, 1929; Colton, 1922; Moore, 1936).

Distribution: North Atlantic Ocean from southern Portugal to Novaya Zemblya [records from the western Mediterranean (Nordsieck, 1968, 1982), Azores, Morocco, Senegal, and Canary Islands (Adanson, 1757) are highly suspect (Cooke, 1915) and need confirmation]; Great Britain; Ireland; Iceland; Greenland; New Jersey, U.S.A., to northern Canada (Abbott, 1974) (For extensive list of geographical range and localities, see Cooke, 1915.)

Genus *Pinaxia* H. & A. Adams, 1853
(Fig. 16A–E)

Pinaxia H. & A. Adams, 1853: 132.
Conothais Kuroda, 1930: 1 [type: *Conothais citrina* Kuroda, 1930, by monotypy].

Type Species: Pinaxia coronata H. & A. Adams, *ex* A. Adams MS, 1853, by monotypy, = *Pinaxia versicolor* (Gray, 1839); synonyms: *Pyrula versicolor* Gray, 1839; ?*Conothais citrina* Kuroda, 1930.

Remarks: Cossmann (1903: 68) allocated section status to *Pinaxia* under *Iopas* (*Iopas*) [= *Nassa*], whereas Thiele (1929: 297) used *Pinaxia* as a section of *Thais* (*Thais*). Wenz (1941: 1121) allotted subgeneric status to *Pinaxia* under *Thais*. Fujioka (1985a: 242) considered *Conothais* congeneric with *Pinaxia*. I agree with Fujioka based on intergrades between *Conothais citrina* and *Pinaxia versicolor.*

Shell: Protoconch (Fig. 16C, D) tall, conical, of about four adpressed whorls, with small subsutural plicae and several microscopic pustules (last whorl), and with outward-flaring lip and sinusigeral notch. Teleoconch (Fig. 16A, B) small, conical to bulbous, smooth, of 4–6 adpressed whorls. Adult shell up to about 25 mm in height, 15 mm in width, with thin,

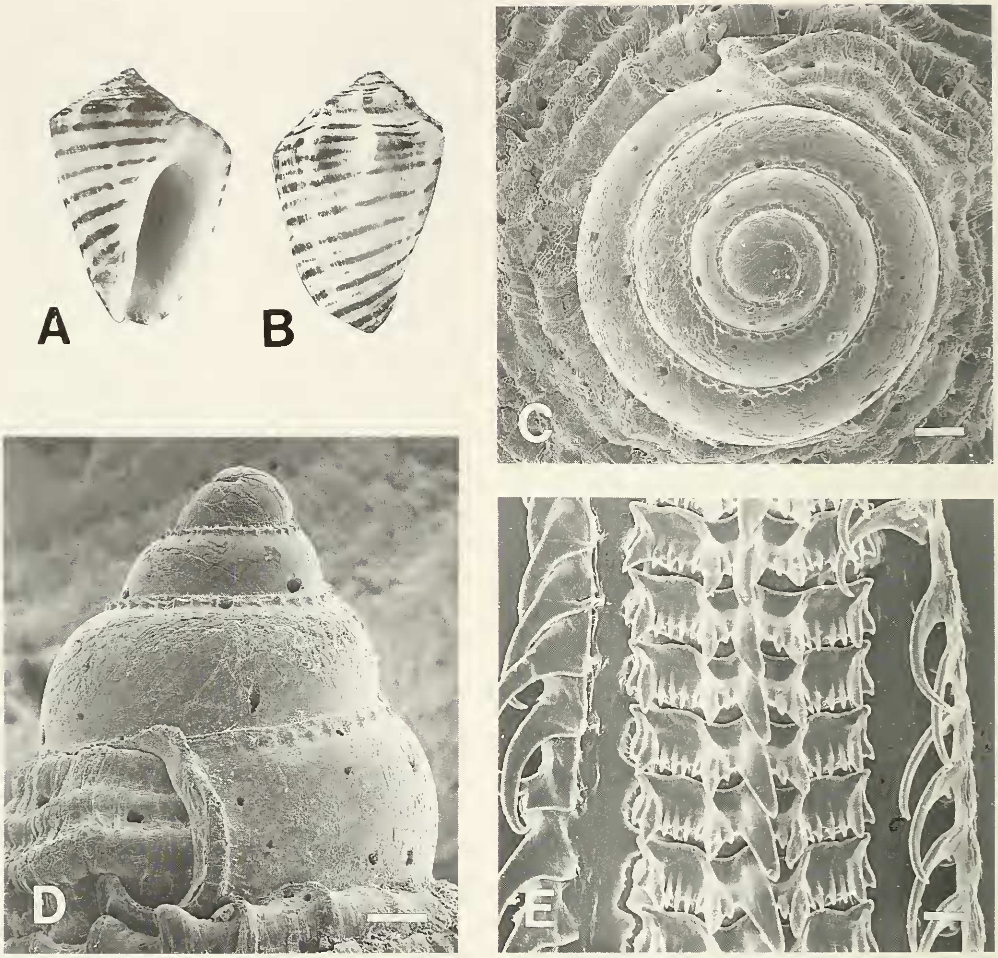

FIG. 16. *Pinaxia versicolor*. A, shell (17 mm), apertural view. B, shell (17 mm), abapertural view. C, protoconch, apical view, SEM (bar = 0.10 mm). D, protoconch, side view, SEM (bar = 0.10 mm). E, radula, SEM (bar = 10 μm).

cream brown periostracum. Body whorl about 90% of shell height, smooth, usually with heavy shoulder with 6–7 inconspicuous wide swellings or knobs. Aperture about 80% of shell height, elongate, narrow. Upper part of thin apertural lip nearly straight, lower end curved. Apertural lip with elongate (4–6 mm) riblets starting about one mm from edge. Anterior siphonal canal a poorly developed notch; posterior siphonal canal absent. Columella nearly straight, margin rounded, with little callus. Siphonal fasciole forming thin, slightly elevated ridge adjacent to callus on lower columella. Shell yellow to orange with 10–11 thin, continuous or discontinuous, spiral, dark brown bands (although banding pattern may be absent); apertural lip and columella yellow to orange brown.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (10–15%); aragonitic layer with crystal planes oriented parallel to growing edge (70–75%); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–25%).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free side with bracket-shaped growth rings; attached side without or with 1–2 bracket-shaped growth lines and with callused, glazed rim (about 30–45% of opercular width) on left.

Anatomy (based on poorly preserved animals only): Head-foot predominantly brown, uniform black at periphery. Cephalic tentacles elongate, brown dorso-centrally, black on periphery, and with white tips. Mantle edge simple, smooth, following contour of aperture, and brown on inside. Siphon long, brown with white specks, extending substantial distance beyond mantle edge. Large accessory boring organ dorsal to ventral pedal gland in females (Fig. 4B).

Osphradium and ctenidium about equal in length; both about equal in width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamella attached along small portion of their base.

Anteriormost portion of ctenidium bending towards anterior portion of osphradium; both equidistant from mantle edge. Anterior ctenidial lamellae wider than deep; posterior lamellae as deep as wide. Lateral and ventral edges concave.

Vaginal opening below and posterior to anal opening. Ventral channel located near left side of capsule gland, consisting of single, hooked flange which originates from ventral epithelium. Large ventral lobe in anterior portion of capsule gland. Ingesting gland between capsule gland and albumen gland. Albumen gland omega-shaped, large, tilted backwards. Low number of white seminal receptacles on dorsal side of albumen gland.

Penis large, slightly recurved, dorsoventrally flattened, elongate, with flagelliform tip. Penial vas deferens as central duct-within-a-duct system occupying about one-third of penis width. Cephalic vas deferens a well-developed duct-within-a-duct system, inconspicuous from outside. Prostate small, closed, solid, yellow, lacking prominent duct, adjacent to narrow, white-walled rectum. Seminal vesicles well developed, golden, orange or white.

Proboscis thinner than gland of Leiblein, unpigmented. Paired accessory salivary glands stubby, club-shaped, short, of equal length, much less than one-half of shell height; left gland completely loose from salivary gland mass; right accessory salivary gland adpressed to salivary gland mass. Salivary glands soft, cottonlike, located dorsally in buccal cavity, larger than accessory salivary glands. Valve of Leiblein elongate, adjacent to salivary gland mass and nerve ring, and with cap structure on anterior end. Salivary ducts attached to anterior portion of esophagus at base of valve of Leiblein. Portion of mid-esophagus with glandular folds long; folds poorly developed. Duct between gland of Leiblein and esophagus as thick as or thicker than posterior esophagus. Esophagus free from gland of Leiblein. Gland of Leiblein spiral, forming one fold between two attached lobes, with central hole for passage of anterior aorta, of hard consistency, yellow, with strawlike outer membrane. Posterior blind duct of gland of Leiblein nearly equal in length to gland itself.

Tubular stomach with about ten folds. Rectal gland not apparent. Small anal opening on tubular extension of rectum. Anal papilla absent.

Radula: Ribbon length about 20–25% of shell height (Fig. 16E). Central cusp on rachidian tooth thin, needle-shaped, straight or bent to either side (artifact?); small backward extension present at central cusp base close to rachidian base; inner lateral denticle on lower half of lateral cusp; outer edge of lateral cusp straight, with one outer denticle on base of lateral cusp, three more well-developed denticles on wide, horizontal marginal edge; lateral cusps nearly equal in length to central cusp; large marginal cusp more than one-half of lateral cusp length; laterally extending lobe on rachidian edge and rachidian base somewhat widened anteroposteriorly. Lateral teeth slender with wide bases, hooked at distal ends, and longer than one-half of rachidian width.

Egg Capsules: Unknown.

Ecology: Pinaxia versicolor lives on intertidal sandflats with rocks and algae. Rehder & Ladd (1973) reported this species from the subtidal zone.

Distribution: Indo-Pacific, from Mauritius (Drivas & Jay, 1987) to Japan (Abbott & Dance, 1982).

Genus *Plicopurpura* Cossmann, 1903
(Fig. 17A–F)

Plicopurpura Cossmann, 1903: 69 (as section of *Purpura*).

Microtoma Swainson, 1840: 72 (*non* Laporte, 1832) [type: *Buccinum patulum* Linnaeus, 1785, by subsequent designation, Herrmannsen, 1847: 42, = *Plicopurpura patula* (Linnaeus, 1758)].

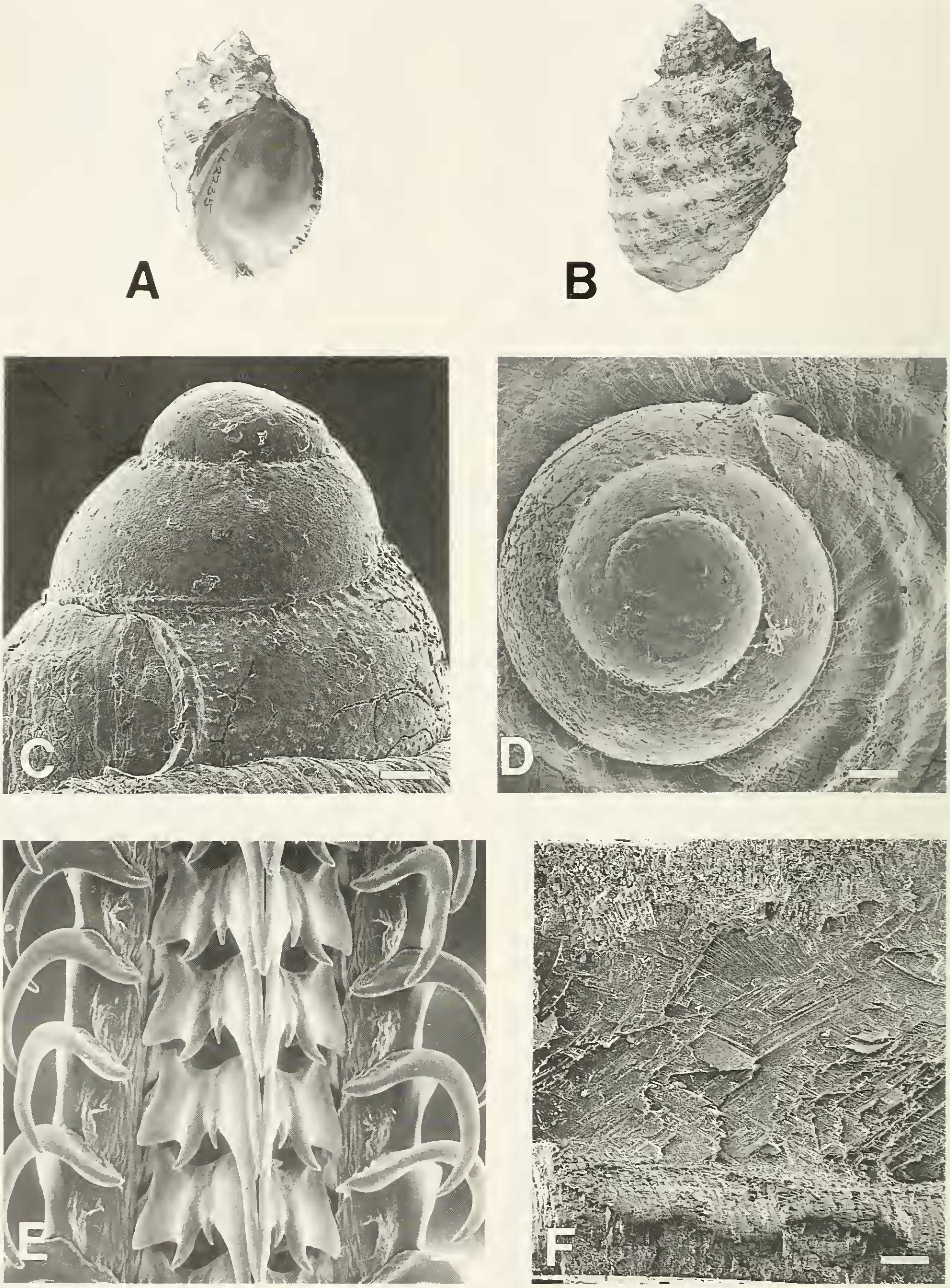

FIG. 17. *Plicopurpura patula.* A, shell (53 mm), apertural view. B, shell (53 mm), abapertural view. C, protoconch, side view, SEM (bar = 70 μm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, radula, SEM (bar = 20 μm). F, shell ultrastructure, SEM (bar = 0.15 mm).

Purpurella Dall, 1871: 110 (*non* Robineau-Desvoidy, 1853, *nec* Bellardi, 1883; as subgenus of *Purpura*) [type: *Purpura columellaris* Lamarck, 1816, by original designation, = *Plicopurpura columellaris* (Lamarck, 1816)].

Microstoma Paetel, 1875: 126 (error for *Microtoma* Swainson).

Patellipurpura Dall, 1909: 50 [type: *Buccinum patulum* Linnaeus, 1758, by monotypy, = *Plicopurpura patula* (Linnaeus, 1758); as section of *Thais*].

Patellapurpura Abbott, 1974: 180 (error for *Patellipurpura* Dall).

Type Species: Purpura columellaris Lamarck, 1816, by original designation, = *Plicopurpura columellaris* (Lamarck, 1816); synonyms: ?*Buccinum patulum* Linnaeus, 1758; *Haustrum dentex* Perry, 1811 [*nomen oblitum;* ICZN, Opinion 886, 1969: 129]; *Purpura pansa* A. A. Gould, 1853.

Remarks: Cossmann (1903: 69) introduced *Plicopurpura,* because the earlier name, *Purpurella* Dall, was preoccupied. Dall (1909: 50) erected *Patellipurpura* for the Caribbean species *patula,* which lacks a columellar fold as found in *Plicopurpura* and placed both *Patellipurpura* and *Plicopurpura* as sections under *Thais.* Thiele (1929: 296) followed Cossmann in recognizing *Plicopurpura* and *Purpura s.s.* as sections of the genus *Purpura,* and synonymized *Patellipurpura* with *Purpura s.s.* (see below). Wenz (1941: 1115) accorded full generic status to *Plicopurpura* and included *Plicopurpura* and *Patellipurpura* as subgenera. Keen (1971b: 552) indicated that *Plicopurpura* is perhaps a nodose subgenus of *Purpura.* Kool (1988b) showed that *Plicopurpura* is sufficiently different from *Purpura* to warrant separate generic status.

Traditionally three species/subspecies were included in this genus: *Plicopurpura columellaris, P. patula,* and *P. patula pansa. Plicopurpura patula* occurs in the Caribbean Province and has been separated from populations in the eastern Pacific since the closure of the Isthmus of Panama; based on the fact that *P. patula* no longer interbreeds with *P. columellaris* in nature, I consider these two taxa separate species on the basis of interrupted gene flow. Keen (1971b: 552) allotted full species status to the two eastern Pacific species: *P. columellaris* and *P. pansa.* However, Wellington & Kuris (1983) provided evidence for conspecificity of these two nominal species. I suspect this species complex to consist of two species: one in the Caribbean, the other in the eastern Pacific (see "Remarks" under treatment of *Stramonita*). Molecular data may demonstrate the actual degree of divergence.

Shell: Protoconch (Fig. 17C, D) moderately tall, conical, of about 2.25 adpressed whorls, with numerous faint subsutural plicae and microscopic pustules (last whorl), with outward-flaring lip and sinusigeral notch. Teleoconch (Fig. 17A, B) large, oval, of 5–6 adpressed whorls, and with high whorl-expansion rate. Adult shell up to about 85 mm in height, 55 mm in width. Body whorl dome-shaped, about 90% of shell height. Body whorl sculptured with 7–8 spiral rows of nodules (most pronounced and nearly spinelike on many juvenile specimens) with four small striae between rows. Aperture wide, oval, about 80% of shell height. Apertural lip smooth on inside, crenate on edge, corresponding to pattern of striae on outside. Anterior siphonal canal a poorly developed notch; posterior siphonal canal well developed in older specimens. Columella flattened, wide, with acute angle of 135° in lower portion. Siphonal fasciole a slightly elevated uneven ridge. Shell grey white to light brown; apertural lip white, with darker areas indicating dark pattern on outside surface; edge of lip caramel brown, with blotched dark brown crenulations; columella caramel brown (sometimes partially white) frequently with sizable dark brown upper parietal blotch.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (30–35%); aragonitic layer with crystal planes oriented parallel to growing edge (10–15%); aragonitic layer with crystal planes oriented perpendicular to growing edge (60–70%) (Fig. 17F). Presence of calcitic layer questionable; scored with "?" in cladistic analysis.

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 4–6 arch- and bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals; Fig. 3A): Head-foot nearly uniform black. Elongate cephalic tentacles black except for white distal tips. Grooved sole of foot yellowish. Mantle edge slightly crenate, following aperture contours. Incurrent siphon black, extending beyond mantle edge. Pedal gland combined with well-developed accessory boring organ (Fig. 4B).

Osphradial length about one-half ctenidial length; osphradial width about one-fifth ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae much wider than deep; posterior lamellae about as deep as wide. Lateral and ventral edge of ctenidial lamellae varying from concave to convex. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening situated on distal end of loose, tubular extension of pallial gonoduct, curled towards mantle or toward buccal mass, and located below and posterior to anal opening. Bursa copulatrix a dorso-ventral chamber connecting with vagina, continuous with capsule gland. Small ventral lobe in anterior portion of capsule gland, lying over ventral channel, which is formed by small, heavily ciliated, circular flange with longitudinal folds and grooves. Capsule gland embedded in spongy connective tissue. Posteriorly, ventral sperm channel divided into two branches: one unciliated, leading into ingesting gland; the other ciliated, leading to albumen gland. Albumen gland omega-shaped. Ingesting gland single- or double-chambered, extending from posterior lower left part of capsule gland to left of anterior part of albumen gland. Seminal receptacles located at dorsal periphery of anterior portion of albumen gland. Females occasionally with minute pseudo-penis.

Penis large, strongly recurved, oval in cross section, tapering distally or with extended, flagelliform tip. Penial vas deferens as duct-within-a-duct system occupying about one-seventh of penial width. Cephalic vas deferens thin, inconspicuous, in straight line from penis to prostate. Prostate closed, directly adjacent to rectum, both embedded in opaque spongy connective tissue. Seminal vesicles well developed, brown.

Proboscis moderately muscular, one-half of gland of Leiblein width, semi-transparent, with pink odontophores (visible in living specimens). Paired salivary glands usually equal in length (but right accessory salivary gland occasionally shorter); both glands elongate, thin, adjacent to salivary glands, about one-third of shell height. Salivary glands often joined, globular in appearance, larger than accessory salivary glands. Salivary ducts attached to anterior portion of esophagus at some distance from valve of Leiblein. Anterior portion of esophagus widened, forming elongate valve of Leiblein, adjacent to salivary glands. Portion of mid-esophagus with glandular folds short, swollen; folds poorly developed. Duct between mid-esophagus and gland of Leiblein well-developed, about equal to posterior esophagus width. Posterior esophagus adjacent to gland of Leiblein, connected to it by connective tissue, or separate. Gland of Leiblein spiral, forming two lobes with dorso-ventral opening for anterior aorta, caramel brown, covered with thick, strawlike outer membrane. Posterior blind duct of gland of Leiblein narrow, elongate, longer than gland itself, and entering dorsal branch of afferent renal vein.

Stomach tubular, with small posterior mixing area with about ten large folds on right two-thirds of interior stomach; left portion smooth. Two digestive diverticula present. Stomach typhlosole and intestinal typhlosole thin. Rectal gland long, thin, dark green, adjacent to entire length of capsule gland. Rectum large in diameter, embedded in spongy connective tissue without separation from capsule gland or rectum by epithelial layer. Anal opening small, well defined, with distinct anal papilla.

Radula: Ribbon length about 45% of shell height (Fig. 17E). Central cusp of rachidian tooth elongate, needle-shaped, with slightly widened base and elongate median slit in central cusp extending from base of rachidian to slightly below tip; small inner lateral denticle separate from but directly adjacent to central and lateral cusps; lateral cusps smooth, with concave outer edge and convex inner edge; outer edge of lateral cusp sloping steeply down to rachidian base. Lateral teeth thin, strongly curved, equal in length to rachidian width.

Egg Capsules: Flat and rounded, up to about 4 mm in width; flat, round top of capsule with central, circular exit hole. Each capsule containing 50–100 eggs measuring about 0.24 mm in diameter (Lewis, 1960). These data are very different from descriptions given by Kool (1989) of *Plicopurpura columellaris*. Because the descriptions of Kool are based on specimens that were collected without the animal that laid them (ANSP 324406), they are probably based on eggs of a different species. The explanation that the egg capsule morphology of the two species is very different appears less likely.

Ecology: Plicopurpura patula occurs from the splash zone and low intertidal to shallow subtidal, on hard substrates (often limestone platforms) in high-energy environments. It feeds on such mollusks as chitons (Clench, 1947; Lewis, 1960; Bandel, 1987; Kool, 1987) and nerites (Britton & Morton, 1989), and also on barnacles (Lewis, 1960; Kool, 1987). As described by Bandel (1987), *Plicopurpura* paralyzes a chiton with a purple staining secretion, pulls it off the substrate, and, while holding it with its foot, eats it. Bandel noted that *Plicopurpura* feeds in the splash zone because the paralyzing secretion would lose much of its effect by dilution when the animal is submerged. However, many rapanines are known to paralyze their prey, yet feed when submerged (Kool, personal observation). Breeding occurs in August and September (Lewis, 1960).

Distribution: Western Atlantic, from central east Florida throughout West Indies to Brazil and Bermuda (Abbott, 1974). Occurrence of a *Plicopurpura*-like shell on Mauritius (Drivas & Jay, 1987) needs further investigation.

Genus *Purpura* Bruguière, 1789
(Fig. 18A–G)

Purpura Bruguière, 1789: 15 (*non* Röding, 1798, *nec* Lamarck, 1799).

Type Species: Buccinum persicum Linnaeus, 1758, by subsequent designation, ICZN, Opinion 886, 1969: 128, = *Purpura persica* (Linnaeus, 1758); synonym: ?*Purpura inerma* Reeve, 1846.

Remarks: The generic name "*Purpura*" was first used by Martini (1777) and subsequently by Martyn (1784) and Meuschen (1787), all of which are non-binominal works. Bruguière formally introduced *Purpura* as a genus in 1789, but did not mention any species. Three years later, Bruguière (1792) included the nominal species *Purpura tubifer* Bruguière, 1792, which would make this the type species by subsequent monotypy. Unfortunately, this taxon is now regarded as a species of *Typhis* Montfort, 1810 (Muricidae: Typhinae). Later, Lamarck (1799, 1801) cited *P. persica* as the sole species in the genus, which did not result in *P. persica* being the type species by monotypy, as Bradley & Palmer (1963: 252) incorrectly stated it to be. To resolve this matter, Bradley & Palmer (1963) and Keen (1964) proposed, by petition to the International Committee of Zoological Nomenclature, that *Purpura persica* be designated type species of *Purpura*. *Purpura persica* officially became the type of *Purpura* after publication of ICZN, Opinion 886 (1969). Detailed nomenclatural history on this genus is given by Dall (1905), Winckworth (1945), Dodge (1956), Bradley and Palmer (1963), and Keen (1964).

Cossmann listed *Purpura persica* as the sole example of the genus *Purpura*. Thiele (1929: 296) incorrectly cited *Purpura patula* as type of *Purpura*, and synonymized *Patellipurpura* with this genus. He recognized the sections *Purpura* and *Plicopurpura* (type species *Purpura columellaris* Lamarck, 1816). Wenz (1941: 1125), and later Pchelintsev & Korobkov (1960: 207), used *Plicopurpura* Cossmann for *Purpura s.l.*, and *Purpura* Martyn for the muricine "*Purpura*" *foliata*. Keen (1971b: 552) synonymized the genera *Plicopurpura* and *Patellipurpura* with *Purpura*. Kool (1988b) argued for separation of *Plicopurpura* and *Purpura*.

Shell: Protoconch (Fig. 18C, E) tall, conical, of about three adpressed whorls [exact count could not be made from available specimen] with outward-flaring lip and sinusigeral notch. Sculptural pattern unknown (due to erosion). Teleoconch (Fig. 18A, B) with high whorl expansion rate, large, heavy, oval, of about six adpressed whorls. Adult shell up to about 115 mm in height, 90 mm in width. Body whorl dome-shaped, about 95% of shell height, sculptured with minute spiral grooves and 7–15 slightly elevated spiral ridges, with one to several less elevated, thinner ridges in between these; surface shiny, appearing smooth. Aperture very wide, oval, about 85% of shell height. Anterior siphonal canal short, wide, open; posterior siphonal canal deep, well developed. Apertural lip smooth, crenate towards edge, corresponding with outside groove pattern. Columella flat to concave, wide with moderate callus layer, with angular curve in lower portion of columella bordering wide, shallow anterior siphonal canal. Siphonal fasciole a slightly elevated ridge, adjacent to columellar callus. Shell grey brown; spiral ridges with color pattern of alternating dark brown and white; dark brown portions of upper two ridges often elevated to form spiral cords of small beads; apertural lip bluish white, with about 30 spiral, dark brown lines

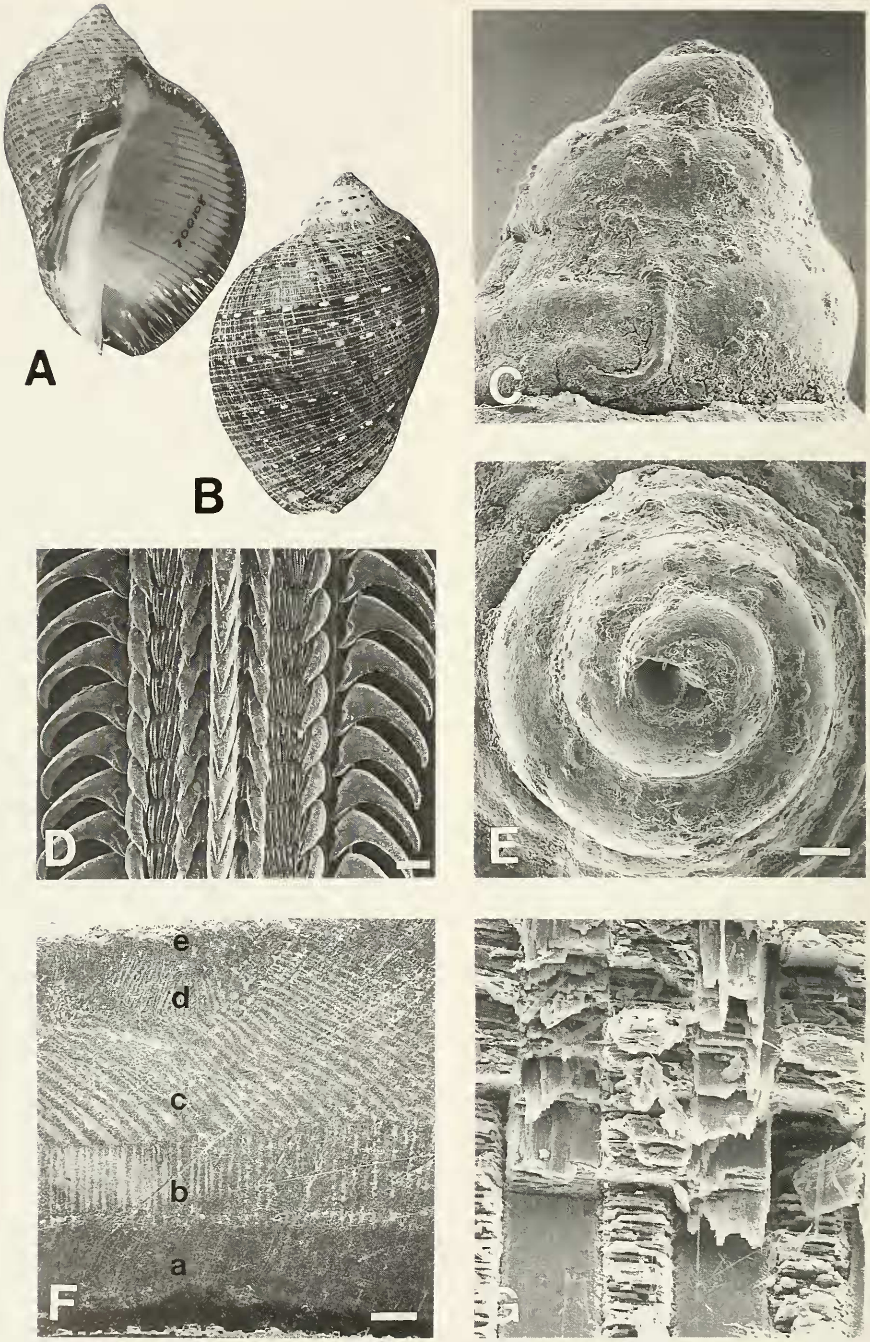

FIG. 18. *Purpura persica*. A, shell (61 mm), apertural view. B, shell (61 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, radula, SEM (bar = 50 μm). E, protoconch, apical view, SEM (bar = 0.10 mm). F, shell ultrastructure, sawed surface, SEM (bar = 0.25 mm); a, aragonite (crystal planes oriented in 45° angle to growing edge); b, aragonite (crystal planes oriented perpendicular to growing edge); c, aragonite (crystal planes oriented parallel to growing edge); d, aragonite (crystal planes oriented perpendicular to growing edge); e, calcite. G, detail of fracture zone of layer b (Figure 18F), SEM (×700).

continuing far into the aperture, with almost uniform, narrow (5–10 mm), black band along edge; columella orange on inside, with blotches of dark brown, cream and blue grey on upper parietal region.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (Fig. 18F, a) (15–25%); aragonitic layer with crystal planes oriented perpendicular to growing edge (Fig. 18F, b, G) (20–25%); aragonitic layer with crystal planes oriented parallel to growing edge (Fig. 18F, c) (35–55%); aragonitic layer with crystal planes oriented perpendicular to growing edge (Fig. 18F, d) (5–15%); calcitic layer (5–10%) (Fig. 18F, e).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 1–2 bracket-shaped growth lines and with callused, glazed rim (about 35–40% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot region flecked with dark brown to black (often in vertical striae) on light yellow background. Elongate tentacles dark brown with light yellow tips. Mantle edge straight, smooth, unpigmented. Incurrent siphon brown black, extending some distance beyond mantle edge. Anterior lobes of foot light brown. Kidney yellowish, not distinct. Accessory boring organ minute, dorsal to pedal gland and located in anteriormost portion of foot.

Osphradial length about one-half ctenidial length; osphradial width between one-fourth and one-third ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes, occasionally more tapered anteriorly. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae much wider than deep; posterior lamellae deeper than wide. Lateral edge of ctenidial lamellae variable; ventral edge concave.

Vaginal opening on tubular extension of pallial gonoduct and located directly below anal opening. Small bursa copulatrix a horizontal slit open to vagina and continuous with capsule gland. Minute ventral sperm channel formed by semi-circular flange originating from the ventral epithelium, located under ventral lobe. Ventral lobe initially small, becoming larger posteriorly, finally disappearing. Posterior ventral channel with one minute flange below larger flange. Lower half of capsule gland opaque; upper portion yellow orange, flocculent. Ingesting gland with several to many sizable chambers surrounded by loose, white connective tissue, extending from left side of capsule gland to albumen gland. Albumen gland omega-shaped, tilted onto posterior half. Seminal receptacles on dorsal periphery of albumen gland. Ovary light brown.

Penis large, strongly recurved, and flattened dorsoventrally at distal end, with large flagellar papilla curved along shaft. Penial duct as duct-within-a-duct system occupying one-third of penial width. Cephalic vas deferens meandering towards prostate. Prostate closed, large, similar to capsule gland in females; embedded in spongy tissue, not distinctly separated from rectum. Small, dark brown seminal vesicles.

Proboscis very large, larger than gland of Leiblein, connected to dorsal wall of buccal cavity with small muscle bundles. Paired accessory salivary glands elongate, thin, equal in length, less than one-half of shell height; right accessory salivary gland loose in right anterior buccal cavity; left gland partially adjacent to salivary gland. Very large salivary glands nearly equal in size to gland of Leiblein and partially located below proboscis. Salivary ducts attached to anterior portion of esophagus close to anterior part of valve of Leiblein. Salivary gland mass partially ventral to proboscis. Valve of Leiblein thin, elongate, adjacent to salivary glands. Portion of mid-esophagus with glandular folds long. Duct between mid-esophagus and gland of Leiblein nearly equal in diameter to posterior esophagus. Posterior esophagus embedded in lower left portion of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, thick, light caramel brown, with strawlike outer membrane. Blind posterior duct of gland of Leiblein much longer than gland itself.

Stomach with large, deep posterior mixing area. Three-fourths of whole posterior mixing area occupied by 25 small folds; anterior one-fourth (adjacent to intestine) smooth, probably non-ciliated. Two large digestive diverticula present. Stomach typhlosole thin. Intestinal typhlosole absent. Rectum thick-walled dorsally, with small internal longitudinal folds; rectum embedded in spongy tissue, separated from capsule gland by distinct layer of epithelium. Anal opening distinct, with upward-pointing papilla at anal opening. Rectal gland moderately wide, extending along entire length of capsule or prostate gland; gland green in females, but usually pink with traces of green in males.

Radula: Ribbon length about 30–35% of shell height (Fig. 18D). Rachidian wide, with needle-shaped central cusp; straight lateral cusps nearly equal in width to central cusp; with or without (can vary within same specimen) single minute denticle on base of inner edge of lateral cusp; outer edge of lateral cusp with one denticle on base; 4–7 well-developed, long, thin denticles on horizontal marginal area; very well-developed marginal cusp nearly equal in size to lateral cusps. Lateral teeth smooth, slightly curved, about three-fourths of rachidian width.

Egg Capsules: Short, dirty yellow, up to 6 mm in height, 5 mm in width, each with flat, widened base; bases usually confluent, capsules occasionally deposited on top of one another; flat, oval top of capsule with central, circular exit hole. Each capsule containing approximately 160–200 eggs measuring about 0.2 mm in diameter (Tirmizi & Zehra, 1983).

Ecology: This species occurs in the rocky subtidal zone (Tirmizi & Zehra, 1983), often in high energy environments (B. Smith, personal communication), where it feeds, among other items, on limpets, as determined from docoglossate rachidian teeth found in gut-content analysis.

Distribution: Indo-Pacific, from Mauritius (Drivas & Jay, 1987) to Marquesas Islands (Salvat & Rives, 1975).

Genus *Stramonita* Schumacher, 1817
(Fig. 19A–F)

Stramonita Schumacher, 1817: 68, 226.

Type Species: Buccinum haemastoma Linnaeus, 1767, by subsequent designation, Gray, 1847: 138, = *Stramonita haemastoma* (Linnaeus, 1767); synonyms: *Thais grisea* Röding, 1798; *Thais metallica* Röding, 1798; *Thais nebulosa* Röding, 1798; *Thais stellata Röding, 1798; Purpura floridana* Conrad, 1837; *Purpura consul* Reeve, 1846; *Purpura forbesii* Dunker, 1853; *Thais floridana haysae* Clench, 1927; *Thais (Stramonita) hidalgoi* Coen, 1946; ?*Thais (Stramonita) langi* Clench, 1948.

Remarks: Most authors have considered *Stramonita* to be a subgenus of *Thais* Röding, 1798 (Cossmann, 1903: 68; Wenz, 1941: 1120; Woodring, 1959: 222; Keen, 1971b: 549). Thiele (1929: 297) placed *Stramonita* as a section of *Thais s.s.*, genus *Thais.* Korobkov (1955: 299) considered *Stramonita* a subgenus of *Thais.* (Kool, 1987: 118) accorded *Stramonita* full generic status. Subspecific status may be accorded to several of the taxa placed in synonymy with *Stramonita haemastoma* ("*Thais*" *haemastoma haysae* Clench, 1927; "*Purpura*" *floridana* Conrad, 1837), but further anatomical, genetic (see Liu et al., 1991), and molecular studies are necessary prior to separation. Based on experiments in the laboratory, Bandel (1976: 118) concluded that *S. floridana* is only an ecological form of *S. haemastoma.*

The tropical eastern Pacific species *Stramonita biserialis* (Blainville, 1832) deserves separate species status because it occurs on the west side of the Isthmus of Panama and has thus been genetically isolated from western Atlantic populations for 2–3 million years (see "Remarks" under treatment of *Plicopurpura*).

Shell: Embryonic shell with pattern of spiral rows of microscopic, volcanolike, cone-shaped pustules. Protoconch (Fig. 19C, D) tall, conical of at least 3.5 adpressed whorls (exact count could not be made from available specimen), with outward-flaring lip; sinusigeral notch covered by teleoconch. First three whorls with faint shoulder with thin ridge sculptured with small plicae; last whorl with shoulder more pronounced and bearing numerous microscopic pustules; numerous small subsutural plicae on each whorl. Teleoconch (Fig. 19A, B) highly variable, fusiform to more oval-shaped, of 7–8 whorls, with varying degree of prominence of suture. Adult shell up to about 90 mm in height, 55 mm in width. Body whorl about 75–85% of shell height, rounded or with distinct shoulder, sculptured with one or two spiral cords with faint knobs and with dense pattern of 30–40 narrow but distinct ridges. Aperture moderately wide, about 60% of shell height. Apertural lip with crenulations continuing into aperture as narrow, tall ridges. Anterior siphonal canal a short, wide notch; posterior siphonal canal present in many adult specimens, but poorly developed, flanked on left by small protrusion of columellar callus. Columella rounded, slightly curved, with little or no cal-

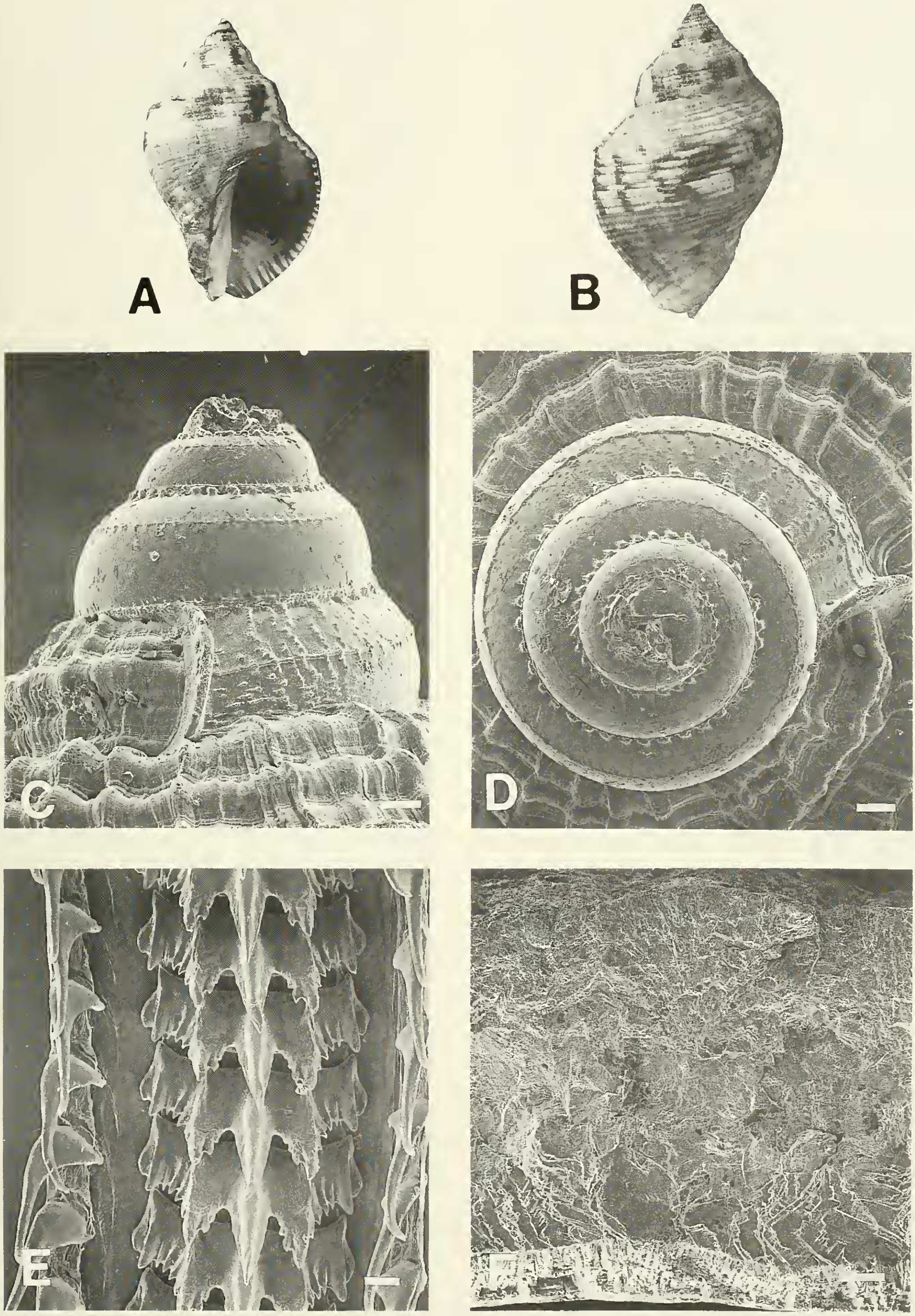

FIG. 19. *Stramonita haemastoma*. A, shell (33 mm), apertural view. B, shell (33 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, radula, SEM (bar = 25 μm). F, Shell ultrastructure, fracture surface, SEM (bar = 0.15 mm).

lus. Siphonal fasciole directly adjacent to callus, with spiral ridge as on rest of whorls. Shell flecked with dark brown, grey, and white, usually forming semi-axial patterns; lower columella white to orange on callused region; upper columella with color pattern similar to that on outside of shell; apertural lip white to orange, with dark brown between distal ends of internal ridges and crenulations.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (10–20%) (lacking in some specimens); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); calcitic layer (40–60%) (Fig. 19F).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 3–5 bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot mottled and blotched with grey black on white background. Cephalic tentacles uniform grey, with black tips. Large mantle covering total head-foot, crenate, with a few, caramel-brown antero-posterior elongate flecks on edge. Incurrent siphon very thick, short, mottled with grey black. Hypobranchial gland pink. Accessory boring organ oval, 2 mm long, with duct (about 4 mm), located dorsal to pedal gland in females (Fig. 4B).

Osphradial length about one-third ctenidial length; osphradial width one-half ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes, or slightly more tapered posteriorly. Osphradial lamella attached along small portion of their base.

Anteriormost portion of ctenidium straight, extending farther anteriorly than osphradium. Anterior and posterior ctenidial lamellae wider than deep. Lateral edges of ctenidial lamellae varying from convex (anterior) to concave (posterior); ventral edges straight.

Vaginal opening a simple hole situated on end of attached tubular extension of pallial gonoduct (in typical *S. haemastoma* morphs; in rounded morphs, vagina more elongate) and located below and slightly anterior to anal opening. Bursa copulatrix extending along entire capsule gland and measuring one-half of gland height. Anterior part of bursa narrow, oriented dorso-ventrally, but circular posteriorly, with intricately branching ridges. Well-developed ventral flange perpendicular to capsule gland lobes, originating from spongy, epithelial tissue on left side of capsule gland or from left lobe of capsule gland. Ingesting gland large, usually black, solid, with material similar to that found in rectal gland. Albumen gland arch-shaped, occasionally with anterior and posterior lobes disjunct to form arch, and with black or white seminal receptacles at periphery. Small, pseudo-penis occasionally present in females.

Penis in males thick, strongly recurved, blunt, dorso-ventrally flattened. Penial vas deferens as duct-within-a-duct system occupying about one-sixth of penial width. Cephalic vas deferens simple, running directly below epithelium. Prostate small, yellow, with wide central duct, adjacent to much larger rectum.

Proboscis thin, long. Paired accessory salivary glands elongate, of equal length, thin, one-third of shell height. Left accessory salivary gland adpressed to salivary gland mass, partially intertwined with it; right accessory salivary gland loose in anterior right buccal cavity, ventral to proboscis. Salivary gland mass equal in size to one accessory salivary gland, located in dorsal buccal cavity between gland of Leiblein and proboscis. Salivary ducts adjacent to esophagus directly anterior to valve of Leiblein. Portion of mid-esophagus with glandular folds long. Mid-esophagus directly attached to gland of Leiblein. Gland of Leiblein of hard consistency, spiraled counterclockwise (forming two "folds" and three "lobes"), enveloped by thin strawlike membrane, varying in color from cream to light brown posteriorly to darker brown anteriorly. Posterior blind duct of gland of Leiblein long, about one-half of gland length, terminating in dorsal branch of afferent renal vein. Posterior esophagus loosely attached to left side of gland of Leiblein.

Stomach large, with several large folds oriented toward intestine. Single large vertical fold with several thin ridges on both sides, perpendicular to and continuous with well-developed stomach typhlosole. Two digestive diverticula present. Intestinal typhlosole well developed, continuing on stomach wall, demarcating intestine from stomach. Several small ridges in intestinal canal. Ciliary movement on stomach wall directed toward intestine. Rectum very wide. Rectal gland green. Anal opening well developed, with pronounced anal papilla.

Radula: Ribbon length about 25% of shell height (Fig. 19E). Rachidian with needle-shaped central cusp; lateral cusps with well-developed inner denticle high on cusp, occasionally with one or two additional denticle(s) below; outside edge of lateral cusp concave, with row of several well-developed denticles continuing up to large marginal cusp; rachidian base with lateral extension. Lateral teeth about equal in length to rachidian tooth.

Egg Capsules: Vase-shaped, large, each with concave and convex sides, up to about 13 mm in height, 2.5 mm in width. Apical plate usually flat or slightly concave, variable in contour, with round to oval, off-center exit hole. Two sutures extending from basal plate of each capsule to apical plate. Capsules arranged in clusters, with concave sides adjacent to convex sides and with confluent bases, each containing 150–800 embryos. Hatching occurs after about 15 days (D'Asaro, 1966). Boone (1984) reported a case of egg capsules attached to floating wood.

Ecology: This species occurs in low- and high-energy intertidal environments. It also lives in mangrove habitats and on *Phragmatopoma* reefs. It feeds on a variety of prey, such as mussels (Burkenroad, 1931), oysters (Bandel, 1976), barnacles (Cake, 1983), and polychaetes (*Phragmatopoma* sp.) (Kool, 1987). A variety of ecological topics was treated by Gunter (1979). I found this species usually to be relatively inactive during low tide, but feeding when submerged at high tide. Females often congregate prior to spawning, which usually occurs from April to May.

Distribution: Eastern Atlantic Ocean, from Mediterranean Sea to West Africa; western Atlantic Ocean, from North Carolina throughout the West Indies to Brazil (Abbott, 1974).

Genus *Thais* Röding, 1798
(Fig. 20A–F)

Thais Röding, 1798: 54.
?*Thalessa* H. & A. Adams, 1853: 127 [type: *Murex hippocastanum* Linnaeus, 1758, by subsequent designation, F. C. Baker, 1895: 183 (Suppressed by ICZN, Opinion 911, 1970: 20), = *Thais aculeata* (Deshayes, 1844)].
?*Menathais* Iredale, 1937: 256 [type: *Purpura pica* Blainville, 1832, by original designation, = *Thais tuberosa* (Röding, 1798)].
?*Thaisella* Clench, 1947: 69 [type: *Purpura trinitatensis* Guppy, 1869, by original designation, = *Thais trinitatensis* (Guppy, 1869)].
?*Reishia* Kuroda & Habe, 1971: 146 [type: *Purpura bronni* Dunker, 1861, by original designation, = *Thais bronni* (Dunker, 1861)].

Type Species: Murex fucus Gmelin 1791, by subsequent designation, Iredale, 1915: 472 (ICZN, Opinion 886, 1969: 128), = *Thais nodosa* (Linnaeus, 1758); synonyms: *Nerita nodosa* Linnaeus, 1758 [*in partem*]; *Murex neritoideus* Linnaeus, 1767 [*in partem*] [also cited as *neritoides* Linnaeus]; *Thais lena* Röding, 1798; *Thais meretricula* Röding, 1798; *Purpura ascensionis* Quoy & Gaimard, 1833.

Remarks: Troschel (1866–1893: 130) placed *Thais* as a subgenus in the genus *Stramonita*. Cossmann (1903) did not list *Thais*. Thiele (1929: 297) included the following subgenera under the genus *Thais: Mancinella*, with sections *Mancinella, Neorapana* and *Tribulus;* and *Thais*, with sections *Thais, Stramonita, Cymia, Pinaxia, Trochia*, and *Agnewia*. Wenz (1941: 1120) included the subgenera *Stramonita, Entacanthus, Cymia, Pinaxia, Trochia,* and *Agnewia* under the genus *Thais.* Fujioka (1985a: 243) recognized both *Reishia* and *Thaisella* as subgenera of *Thais.*

Iredale (1915: 472) provided a type species designation ("*Thais neritoides* = *Murex fucus* Gmel") in a synopsis of Dall's (1909) work. Stewart (1927: 386) listed *Thais fucus* as type species of *Thais* but recognized *Thais nodosa* as a valid name by explaining that *Murex neritoideus* was an unnecessary substitute for *Nerita nodosa* Linnaeus, both being based on the same figures. Stewart then synonymized the nominal species *fucus, neritoideus, lena,* and *nodosa.* In 1937 (p. 256) Iredale listed ". . . *Thais lena* Bolten [*sic*] = *Murex fucus* Gmelin, . . ." as the type species, with this type species fixed as *Murex fucus* Gmelin, 1791, by subsequent designation by Iredale (1915) (ICZN, Opinion 886, 1969: 128). Furthermore, the nominal species *nodosa,* the oldest available name, acquired official status in the same opinion.

Thais nodosa meretricula from Ascension Island is herein considered synonymous with *Thais nodosa nodosa*. The number of black dots on the columella, often cited as a distinctive character for separating the two forms, is

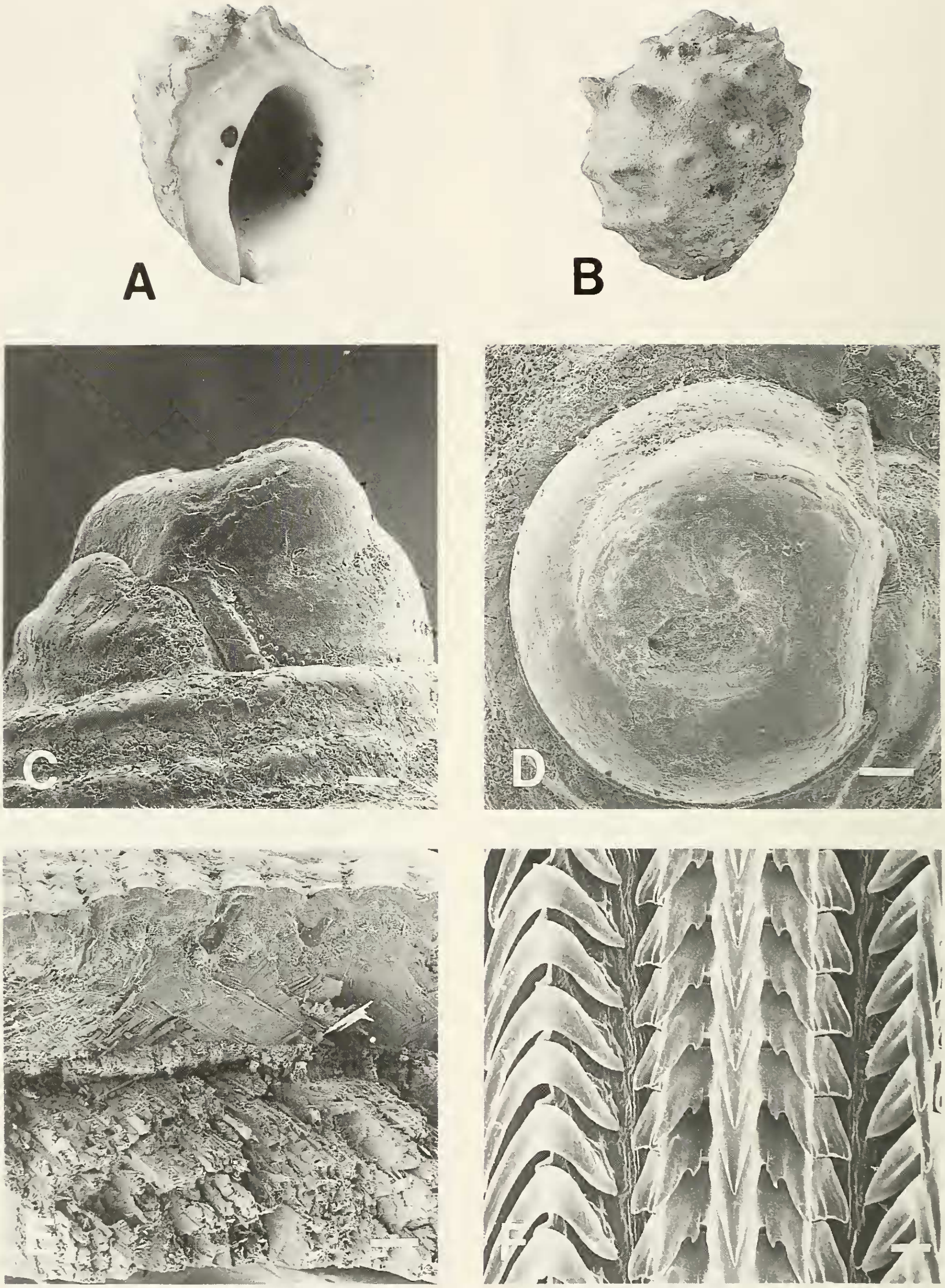

FIG. 20. *Thais nodosa*. A, shell (45 mm), apertural view. B, shell (25 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, fracture surface, SEM (bar = 0.50 mm). F, radula, SEM (bar = 25 μm).

variable in both and shows overlap. Specimens from the African mainland are usually nodose, whereas most, but not all, specimens from Ascension Island are smooth.

Shell: Protoconch (Fig. 20C, D) conical, of at least two adpressed whorls (exact count could not be made from available specimen), and with outward-flaring lip; sinusigeral notch covered by teleoconch. Sculptural pattern obscured by erosion, except for several microscopic pustules observed around lip region. Teleoconch (Fig. 20A, B) with high whorl expansion rate, large, ovate to nearly round, of 4–5 adpressed whorls. Adult shell up to about 70 mm in height, 55 mm in width (form *meretricula* has the largest representatives). Body whorl dome-shaped, usually exceeding 95% of shell height, occasionally with aperture reaching beyond apex. *Thais nodosa* form *nodosa* sculptured with five (sometimes four) spiral rows of 8–9 knobs (occasionally spinelike) and with about 35 narrow, low, spiral ridges, 4–6 of them between rows of knobs; knobs on second and third rows largest. *Thais nodosa* form *meretricula* with rounded body whorl sculptured with about 35 narrow, low spiral ridges. Both forms with wide, oval aperture usually exceeding 95% of shell height. Apertural lip thick, with crenulations on edge corresponding to ridge pattern on outer surface; inside smooth and polished. Anterior siphonal canal as poorly developed notch; posterior siphonal canal poorly developed in most specimens, well developed in others. Columella with wide, flat, heavily callused parietal region and with moderately angular curve in lower region. Siphonal fasciole a well-developed ridge lying behind callus on lower parietal region. Shell dirty white to brown, columella white, with 1–4 large brown black spots (although overlap occurs, usually 1–2 in *Thais nodosa* form *nodosa;* 3–4 in *T. nodosa* form *meretricula*) arranged in vertical row; aperture and apertural edge white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (30–50%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–15%); aragonitic layer with crystal planes oriented parallel to growing edge (20–25%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–10%); calcitic layer (5–10%) (Fig. 20E).

Operculum: D-shaped, with lateral nucleus in center right (Fig. 1C). Free side with bracket-shaped growth lines; attached side with about 4–6 bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot and long cephalic tentacles mottled with black. Mantle edge straight, simple, following contour of aperture. Anterior siphon extending substantial distance beyond mantle edge. Sole of foot a pattern of pustules and ridges. Nephridial gland yellow. Kidney grey brown. Accessory boring organ dorsal to pedal gland in females (Fig. 4B).

Osphradial length slightly more than one-half ctenidial length; osphradial width slightly less than ctenidial width. Osphradium symmetrical in shape along lateral axis; right pectin distinctly wider than left one. Osphradial lamellae deeper than wide, attached along very small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae deeper than wide. Lateral edge of ctenidial lamellae varying from concave (anterior) to straight or convex (posterior); ventral edge varying from slightly concave (anterior) to distinctly concave (posterior).

Vaginal opening round, situated on posteriorly curved tubular extension of pallial gonoduct and located directly below anal opening. Ventral flange small, crescent-shaped, originating from ventral epithelium. Ventral channel under large ventral lobe. Ingesting gland on left and posterior sides of capsule gland. Several seminal receptacles on dorsal periphery of omega-shaped albumen gland.

Penis strongly recurved, dorso-ventrally flattened, with short thick flagelliform tip (Fig. 5D). Vas deferens as tube-within-a-tube system occupying about one-fifth of penial width. Prostate white yellow, embedded in spongy connective tissue, with closed duct, similar to capsule gland in females. Seminal vesicles pale yellow.

Proboscis very large, about equal in width to gland of Leiblein. Paired accessory salivary glands thin, long, less than one-half of shell height; right gland usually few millimeters longer than left; left gland intertwined with salivary gland mass, right gland free of salivary gland mass and located ventrally in anterior buccal cavity. Salivary gland mass in dorsal buccal cavity. Valve of Leiblein small, elongate, adjacent to salivary gland mass. Salivary ducts attached to anterior portion of esophagus close to anterior part of valve of Leiblein. Duct between mid-esophagus and gland of Leiblein not pronounced. Posterior esophagus adjacent to lower left gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, dark brown with thin but distinct strawlike membrane. Posterior blind duct of gland of Leiblein more than one-half of gland length.

Tubular stomach smooth or with many small folds oriented toward center. Stomach with two digestive diverticula, but without intestinal typhlosoles (possibly not visible due to bad preservation). Rectal gland long, green. Anal opening small, indistinct, with anal papilla equal in size to opening.

Radula: Ribbon length about 30% of shell height (Fig. 20F). Rachidian with wide central cusp; inner edge of lateral cusp straight to convex, with large denticle at base; outer edge of lateral cusp straight or concave, with 1–2 small denticles on base; 1–2 more denticles on slightly sloping marginal edge; marginal cusp large. Lateral teeth about equal in length to rachidian width.

Egg Capsules: Unknown.

Ecology: Thais nodosa lives in the rocky intertidal zone (Rios, 1970; Abbott & Dance, 1982).

Distribution: Eastern Atlantic, from western Africa (Bernard, 1984), to Ascension Island (Rosewater, 1975) and Cape Verde Islands (Nordsieck, 1968); western Atlantic, Fernando de Noronha Island, off Brazil (Rios, 1970).

Genus *Tribulus* Sowerby, 1839
(Fig. 21A–E)

Tribulus (Klein) Sowerby, 1839: 107.
Planithais (Bayle) Fischer, 1884: 645 [type: *Purpura planospira* Lamarck, 1822: 240, by monotypy, = *Tribulus planospira* (Lamarck, 1822)].

Type Species: Purpura planospira Lamarck, 1822, by monotypy, = *Tribulus planospira* (Lamarck, 1822); synonyms: *Haustrum pictum* Perry, 1811 [rejected name; ICZN, Opinion 886, 1969: 129]; *Purpura lineata* Lamarck, 1816 [*nomen oblitum,* Old, 1964: 48].

Remarks: Sowerby (1839) formally introduced this name taken from an unpublished manuscript by Klein. H. & A. Adams (1853: 126) used *Tribulus* as a subgenus of *Purpura.* Cossmann (1903: 68) listed *Tribulus* (as *Planithais*) as a section of *Purpura s.s.;* Thiele (1929: 297) gave it section rank under *Mancinella s.s.;* Wenz (1941: 1118) included *Tribulus* as a subgenus of *Mancinella,* whereas Keen (1971b: 550) placed it under *Thais.* Old (1964: 47–48) pointed out that the nominal species *pictum* Perry, 1811 (see above), and *lineata* Lamarck, 1816, are *nomina oblita.* Therefore, Lamarck's taxon *Purpura planospira,* which he based on his own drawing of *P. lineata,* is the valid name and the type species of *Tribulus* by monotypy.

Shell: Protoconch (Fig. 21C, D) tall, conical, of 3.5–4 adpressed whorls and with outward-flaring lip; sinusigeral notch obscured by teleoconch. Sculptural pattern obscured by erosion. Teleoconch (Fig. 21A, B) large, oval to nearly round, of 3–4 adpressed whorls; dorsal sides of last whorls forming flat plateau. Adult shell up to about 75 mm in height, 60 mm in width. Body whorl and aperture reaching beyond apex. Body whorl dome-shaped, sculptured with 1–5 wide, low, spiral ridges between six lamellose, high ridges; first three adapical ridges most pronounced, top two most adjacent to each other. Apertural opening very wide, oval, usually reaching total shell height or extending beyond shell spire. Apertural lip thick, with elongate denticles on edge corresponding to ridge pattern on outside surface; inside smooth and polished, with traces of denticle pattern from previous growth stages. Anterior siphonal canal a wide, completely open notch; posterior siphonal canal absent. Columella concavely curved. Parietal region very wide, heavily callused, with large, deep, central indentation which partially excavates parietal region; several elongate denticles on lower portion of parietal region. Siphonal fasciole as ridge, resembling fifth and sixth body whorl ridges, lying behind callused lower portion of columella. Shell dirty white to uniform orange brown to dark brown; columella white, with orange brown blotches and black streak in white indentation of parietal region; denticles on columella and apertural lip orange brown, remainder of lip white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (10–15%) (lacking in many specimens);

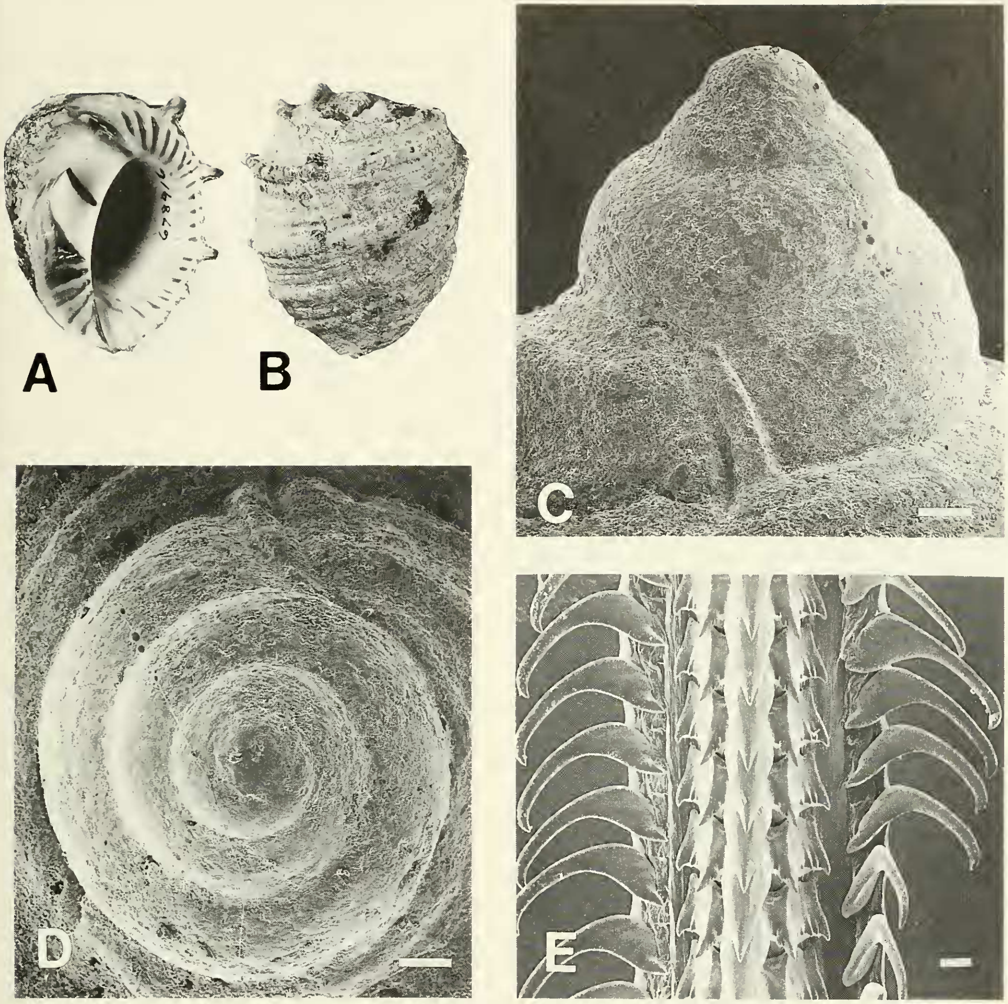

FIG. 21. *Tribulus planospira*. A, shell (50 mm), apertural view. B, shell (50 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, radula, SEM (bar = 35 μm).

aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (25–30%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–10%); calcitic layer (25–30%).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 4–6 bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on poorly preserved male animals; no female specimens available): Head-foot red brown. Anterior siphon dark brown, extended some distance from mantle edge. Small accessory boring organ dorsal to small pedal gland (Fig. 4B).

Osphradial length about one-half ctenidial length; osphradial width less than one-half osphradial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along very small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae wider than deep. Lateral edge of ctenidial lamellae varying from straight to concave; ventral edge straight.

Penis strongly recurved, with long flagellum recurved along penial shaft. Penial vas deferens as centrally located duct-within-a-duct system occupying about one-fifth of penis width. Seminal vesicles well developed, golden brown.

Proboscis unpigmented, narrower than gland of Leiblein. Accessory salivary glands thin, long. Salivary gland mass light brown, larger than accessory salivary glands. Gland of Leiblein spiral, caramel-brown, with straw-like external membrane. Mid-esophagus directly attached to gland of Leiblein over small portion. Posterior esophagus adjacent to left lower gland of Leiblein. Anal opening well developed, with anal papilla attached to wall.

Radula: Ribbon length about 30% of shell height (Fig. 21E). Rachidian with very wide central cusp, constricted at base; inner edge of lateral cusps straight to convex, with single denticle at base; outer edge of lateral cusps straight to concave, with several small denticles at base; base of outer edge of lateral cusp concavely sloping to large marginal denticle. Lateral teeth thin, smooth, longer than width of rachidian.

Egg Capsules (identification uncertain; deposited on valve of a pectinid, USNM 96840; egg capsule size corresponding with size of pedal gland): Small, laterally flattened, up to 4.5 mm in height, each capsule rectangular in cross section, consisting of four distinct plates: front and back plate 2–2.5 mm in width, side plates 0.5–1 mm in width; front plate vase-shaped, side plates of equal distance along total surface with central exit hole separating side plates. Capsule attached by all sides (stalk absent). Capsules deposited in row, with front plates adjacent to back plates.

Ecology: Tribulus planospira lives on vertical hard substrates in the high-energy intertidal zone (J. H. McLean, personal communication).

Distribution: Eastern Pacific, from Cabo San Lucas, Mexico, to Ecuador (Keen, 1971b) and Galápagos Islands (Sabelli & Tommasini, 1979).

Genus *Vasula* Mörch, 1860
(Fig. 22A–E)

Vasula Mörch, 1860: 99 (as a subgenus of *Purpura*).

Vascula Woodring, 1959: 223 (error for *Vasula* Mörch) (as a subgenus of *Thais*).

Type Species: Purpura melones Duclos, 1832, by monotypy, = *Vasula melones* (Duclos, 1832); synonym: *Purpura crassa* Blainville, 1832.

Remarks: Cossmann, Thiele and Wenz did not use this name. Keen (1971b: 550) allotted *Vasula* subgeneric status under *Thais,* following Woodring (1959: 223).

Shell: Protoconch of about 3.5 whorls, otherwise unknown. Teleoconch (Fig. 22A, B) solid, squat, elongate-ovate, of 6–7 adpressed whorls. Adult shell up to about 50 mm in height, 35 mm in width. Body whorl about 90% of shell height, globose, but often with heavy shoulder and straight side, and sculptured with numerous (35–45) fine, nearly equidistant, spiral grooves; otherwise smooth. Apertural opening moderately wide, about 75–80% of shell height. Apertural lip rounded or J-shaped, depending on development of shoulder; inside smooth and polished, crenate on edge. Anterior siphonal canal a short, wide notch; posterior canal poorly developed. Columella rounded, nearly straight, with moderate callus layer. Siphonal fasciole forming slightly elevated ridge, slightly covered with callus on upper part. Shell dark brown with continuous or discontinuous spiral patterns of white blotches; columella pigmented with light brown, pink, white, yellow and/or orange; apertural lip whitish yellow, often with pinkish tint, and with narrow continuous or discontinuous black band along edge.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (10–15%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (55–60%) (Fig. 22C). Presence of calcitic layer questionable.

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot mottled black; tentacles black on proximal half of distal tips. Mantle edge smooth. Long anterior siphon extending far beyond mantle edge. Digestive gland car-

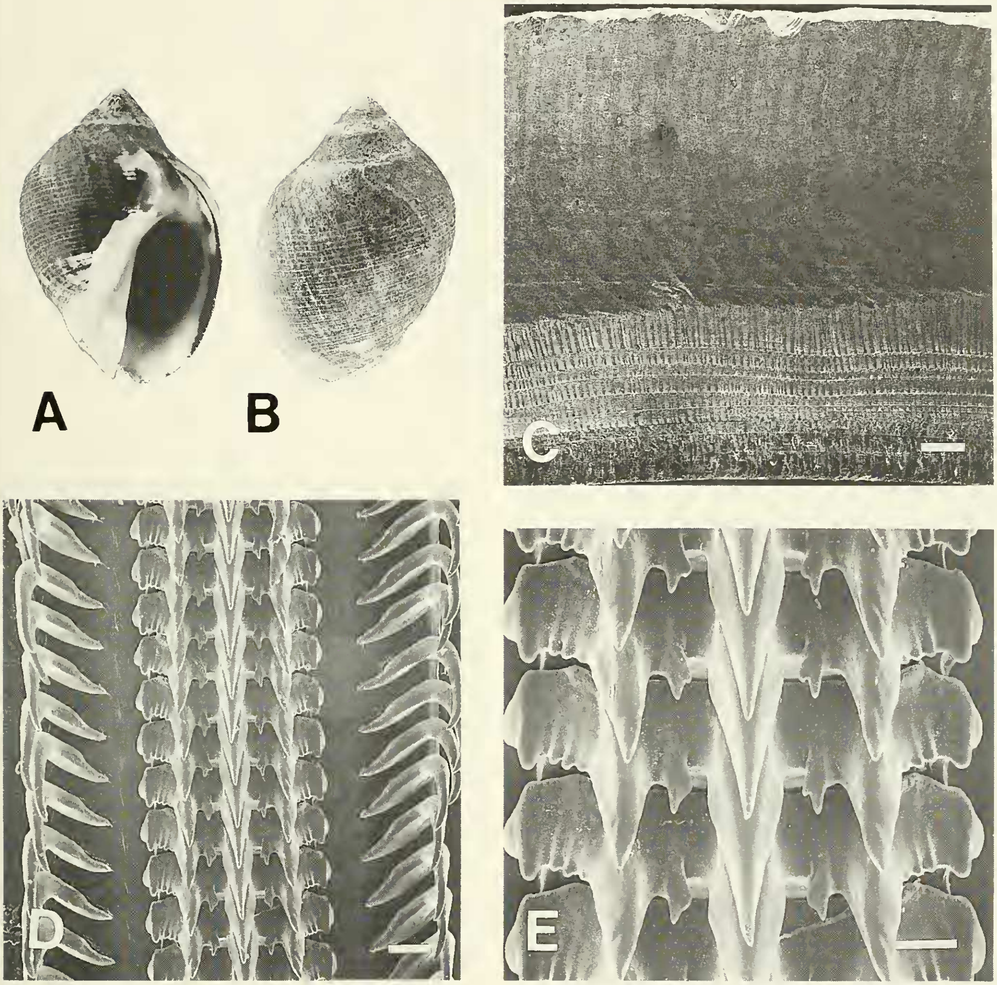

FIG. 22. *Vasula melones*. A, shell (45 mm), apertural view. B, shell (45 mm), abapertural view. C, shell ultrastructure, polished fracture surface, SEM (bar = 0.20 mm). D, radula, SEM (bar = 35 μm). E, radula, rachidian row, SEM (bar = 20 μm).

amel-brown. Well-developed, elongate accessory boring organ close to foot sole.

Osphradial length slightly more than one-half ctenidial length; osphradial width slightly more than ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae deeper than wide. Lateral and ventral ctenidial lamellae concave.

Vaginal opening enlarged, protruding from short, tubular extension of pallial gonoduct, and located below and slightly posterior to anal opening. Bursa copulatrix as dorso-ventral slit connected to vagina, continuous with capsule gland. Large hook-shaped, ventral flange originating from ventral epithelium, located under ventral lobe of capsule gland, and minute posteriorly. Ingesting gland slightly dorsal to posterior portion of capsule gland, with many very small chambers filled with black granular material. Seminal receptacles on dorsal periphery of omega-shaped albumen gland.

Penis large, strongly recurved, with elongate flagelliform tip. Penial vas deferens as duct-within-a-duct system. Testis whitish.

Proboscis unpigmented, about as wide as gland of Leiblein. Paired accessory salivary glands long, thin, about one-half of shell height; left gland adjacent to proboscis and left salivary gland, right gland in anterior part of buccal cavity adjacent to proboscis and right salivary gland. Salivary glands separated by withdrawn proboscis. Duct between mid-esophagus and gland of Leiblein very short. Posterior esophagus adjacent to lower left side of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of soft consistency, light brown, without strawlike membrane.

Stomach thin-walled, with 20–30 thin, nearly parallel folds and small folds, each oriented towards stomach center. Several microscopic folds on small portion of posterior mixing area adjacent to intestine. Large stomach typhlosole as thin flange partially lying over small folds. Two digestive diverticula present. Intestine smooth-walled, with wide intestinal typhlosole and very thin folds in intestinal groove. Thin-walled, wide rectum with small crystals and black granular material. Rectal gland dark green to black, adjacent to most of capsule gland in females. Small papilla above small but distinct anal opening.

Radula: Central cusp on rachidian constricted at base (Fig. 22D, E); lateral cusps straight; inner denticle small (occasionally bicuspid) and nearly free from lateral cusp; several small marginal denticles at base of lateral cusp, on narrow, somewhat sloping marginal area; marginal cusp pronounced, larger than marginal denticles; rachidian base with lateral extension. Lateral teeth smooth, nearly total rachidian width.

Egg Capsules: Unknown.

Ecology: During low tide, animals were found in shady areas on groups of rocks and boulders overgrown with barnacles and different species of oysters.

Distribution: Eastern Pacific, from Mexico to Peru and Galápagos Islands (Keen, 1971b).

Genus *Vexilla* Swainson, 1840
(Fig. 23A–E)

Vexilla Swainson, 1840: 300.
Provexillum Hedley, 1918: 93 [type: *Strombus vexillum* Gmelin, 1791, by monotypy, = *Vexilla vexillum* (Gmelin, 1791)].

Type Species: Vexilla picta Swainson, 1840, by monotypy, = *Vexilla vexillum* (Gmelin, 1791); synonyms: *Strombus vexillum* Gmelin, 1791; *Purpura taeniata* Powys & Sowerby, 1835.

Remarks: Swainson (1840: 300) placed this genus in the subfamily Nassinae. Cossmann (1903: 68) considered *Vexilla* a valid genus; Thiele (1929: 296) placed it as a subgenus under *Nassa* (*Jopas*). Wenz (1941: 1117) followed Thiele's arrangement but used *Nassa* instead of *Jopas*. Most recent authors recognized this genus.

Shell: Protoconch (Fig. 23D, E) very short, domelike, of about two adpressed whorls, sculptured with small subsutural plicae on last whorl, and with outward-flaring lip; sinusigeral notch obscured by teleoconch. Teleoconch (Fig. 23A, B) elongate-oval, of 3–4 adpressed whorls. Adult shell up to about 25 mm in height, 15 mm in width. Body whorl rounded, elongate, smooth, up to about 95% of shell height. Apertural opening elongate, about 80% of shell height. Apertural lip slightly curved to J-shaped; inside of apertural lip smooth, polished, with crenulations on edge continuing inward as small ridges for short distance. Anterior siphonal canal a poorly developed notch. Posterior siphonal canal flanked on left by small protrusion of columellar callus. Columella rounded to flat, with little callus, curving inward at lower portion. Siphonal fasciole forming slightly elevated ridge. Shell usually colored with eight pairs of dark brown and cream, narrow, spiral bands; cream bands occasionally with reddish narrow line in center. Columella and parietal region white, sometimes with light or dark brown streak on lower end, occasionally continuing upward along inside of columella; interior apertural lip white, with faint, light brown lines (traces of color pattern on edges of previous growth stages); edge white with faint light brown blotches between crenulations and denticles corresponding to banding pattern on outside shell surface.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (30–35%); aragonitic layer with crystal planes oriented parallel to growing edge (40–45%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%).

Operculum: Ovate-elongate, tapered at lower end, with lateral nucleus in upper right (Fig. 1E). Free surface without distinct growth

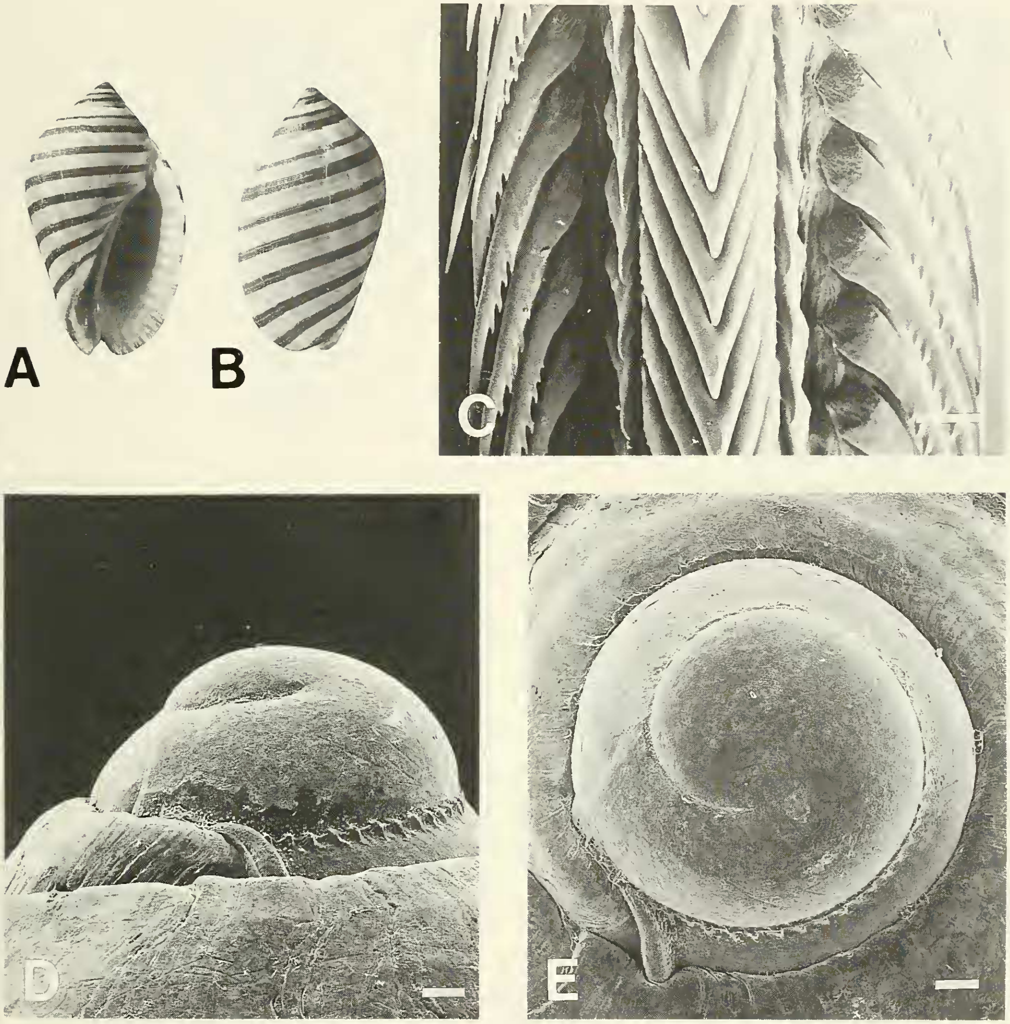

FIG. 23. *Vexilla vexillum.* A, shell (14 mm), apertural view. B, shell (14 mm), abapertural view. C, radula, SEM (bar = 20 μm). D, protoconch, apical view, SEM (bar = 50 μm). E, protoconch, side view, SEM (bar = 50 μm).

lines; attached surface also without distinct growth lines and with callused, glazed rim (about 45–50% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot mottled dark brown on opaque grey. Cephalic tentacles long, mottled dark brown on grey, with many white dots, white at tips. Mantle edge simple, straight. Anterior siphon long, extending beyond mantle edge. Nephridial gland thin, short, dorsal to heart. Females with small, shallow ventral pedal gland close to anterior part of foot. Boring organ apparently absent. Sole of foot with small, shallow pustules.

Osphradial length slightly more than one-half ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae triangular, attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae deeper than wide, or as deep as wide. Lateral edge of ctenidial lamellae concave; ventral edge straight.

Vaginal opening an elongated slit below and slightly posterior to anal opening. Semicircular ventral flange (originating from epithelium) located below right lobe. Albumen gland omega-shaped, with white, silvery seminal receptacles on dorsal periphery of albumen gland.

Penis flagelliform, slightly recurved, oval in cross section, folded at gradually tapering tip. Penial duct as minute duct-within-a-duct system occupying one-eight of penial width. Cephalic vas deferens minute, inconspicuous. Pallial vas deferens appearing open to mantle cavity (in specimens from USNM 718391) or closed (in specimens from Hawaii). Prostate solid, with ventral duct, adjacent to rectum. Seminal vesicles white.

Proboscis short and wide, equal in width to gland of Leiblein. Accessory salivary glands absent. Two large, orange (white in USNM 718391) distinctly separated salivary glands, one between proboscis and gland of Leiblein, other in right anterior part of buccal cavity; both glands in dorsal buccal cavity, multilobular. Valve of Leiblein short, with caplike structure on anterior end continuing smoothly into anterior portion of esophagus, some distance from nerve ring and adjacent to left salivary gland. Salivary ducts attached to anterior portion of esophagus at considerable distance from valve of Leiblein. Mid-esophageal folds inconspicuous (possibly due to overall poorly developed, thin esophagus). Duct between mid-esophagus and gland of Leiblein short, thinner than esophagus itself. Posterior esophagus loose from gland of Leiblein, occasionally looped at anteriormost fold of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, brown (yellowish white and soft in specimens from USNM 718391), lacking strawlike outer membrane. Posterior duct of gland of Leiblein shorter than gland itself, terminating in dorsal branch of afferent renal vein.

Stomach as wide, U-shaped tube with several to many folds on stomach wall of posterior mixing area oriented toward center of stomach. Two digestive diverticula present. Stomach typhlosole lacking or poorly developed, located some distance from posterior mixing area edge, thus interrupting folds. Intestinal typhlosole distinct. Rectal gland thin, along entire capsule gland or prostate. Anal opening inconspicuous, with large anal papilla.

Radula: Ribbon length about 25% of shell height (Fig. 23C). Rachidian tooth with extremely wide central cusp extending along most of rachidian base; few small serrations at base of side of central cusp; lateral cusps smooth, one-third of central cusp length, sloping down toward edge of rachidian. Lateral teeth serrated along nearly entire length, much longer than rachidian width.

Egg Capsules: Unknown.

Ecology: This species occurs on high-energy rocky shores in the low intertidal zone on the sea urchins *Colobocentrotus* and *Echinometra* on which it feeds (Kay, 1979; Kool, 1987: 120).

Distribution: Indo-Pacific, from eastern Africa (Kilburn & Rippey, 1982) to Hawaii (Kay, 1979).

Descriptions of Taxa Traditionally Considered Belonging to Outgroups of Thaididae/nae of Authors

To evaluate taxonomic positions of the taxa described above at the subfamilial and familial levels, and to examine the boundaries of monophyletic groups, other muricid taxa, not believed to be in Thaididae/nae of authors, were studied and scored for the same characters. Choice of taxa depended on such criteria as availability and previous taxonomic placement. For example, *Muricanthus fulvescens* represents the Muricinae, *Rapana rapiformis* the Rapaninae of authors, and *Forreria belcheri* is a taxon *incertae sedis.*

Muricanthus fulvescens (Sowerby, 1841)
(Fig. 24A–F)

Shell: Protoconch (Fig. 24C, F) very tall, conical, of 4.5–4.75 adpressed whorls, with outward-flaring lip and sinusigeral notch. First two whorls smooth, later whorls with microscopic pustules. Protoconch I nearly as wide as first whorl of Protoconch II. Teleoconch (Fig. 24A, B) very large, wide, fusiform, multispined, of about eight whorls, with impressed suture, and with long, well-developed siphonal canal. Adult shell up to about 185 mm in height, 105 mm in width. Body whorl about 85–90% of shell height, sculptured with 7–9 varices, each with about ten spiny knobs open on anterior side. Knobs on varices inter-

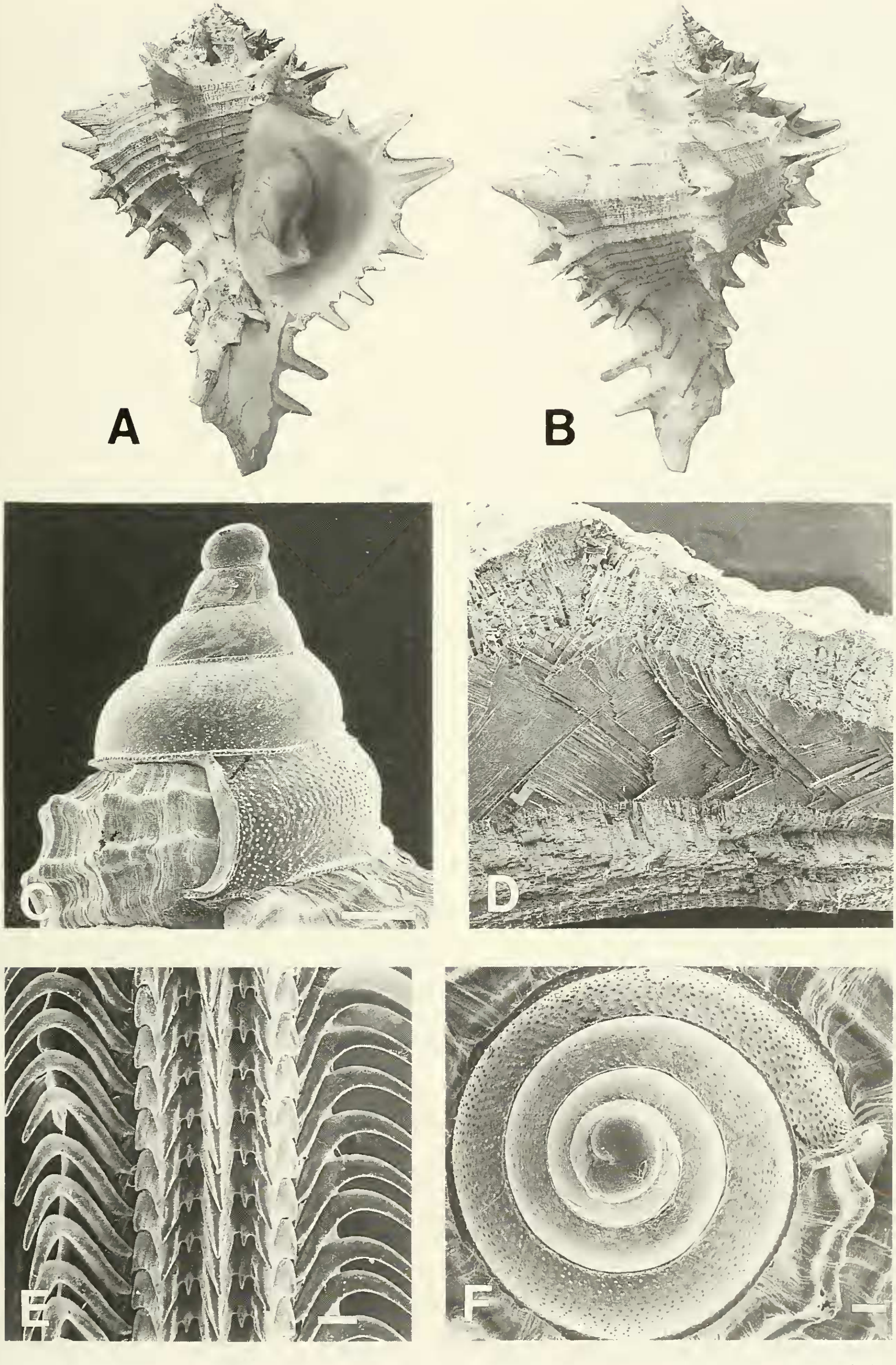

FIG. 24. *Muricanthus fulvescens*. A, shell (136 mm), apertural view. B, shell (136 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.25 mm). D, shell ultrastructure, fracture surface, SEM (×35). E, radula, SEM (bar = 50 μm). F, protoconch, apical view, SEM (bar = 0.10 mm).

connected by folds and ridges. Apertural opening round; aperture (including anterior siphonal canal) about 70% of shell height. Apertural lip semi-circular, thin, except when enforced with knobs on varix; inside smooth and shiny; crenulations on edge elongated, continuous with row of small denticles. Anterior siphonal canal long, wide, almost completely closed, straight, without callus, about 40–45% of shell height; posterior siphonal canal absent. Columella rounded, parietal region narrow, with moderate callus layer, occasionally partially detached at margin. Siphonal fasciole well developed, with former distal ends of siphonal canal forming angle with one another. Shell whitish yellow with light and dark brown spiral, continuous or discontinuous lines and blotches; columella and apertural lip white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (30–40%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%) (Fig. 24D).

Operculum: Ovate, with terminal nucleus in lower right (Fig. 1A). Free surface with concentric growth lines; new growth often partially overlapping previous growth, resulting in lamellose surface; attached surface with many (about 30–50) fine growth lines following contour of operculum and with very heavily callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals): Anterior siphon not extending beyond mantle edge. Digestive gland and kidney green. Accessory boring organ well developed, short distance form sole of foot in males, combined with well-developed pedal gland in females (Fig. 4B).

Osphradial length slightly less than one-third ctenidial length; osphradial width one-third to one-half ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, usually extending farther anteriorly than osphradium. Anterior and posterior ctenidial lamellae much wider than deep. Lateral and ventral edge of ctenidial lamellae varying from concave to convex. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening a slit situated on distal portion of tubular extension of pallial gonoduct and located directly below anal opening. Bursa copulatrix as large diverticulum. Ventral flange long anteriorly, originating from left lobe of capsule gland, and minute posteriorly. Large ingesting gland on left side of posterior portion of capsule gland extending to albumen gland and consisting of many small chambers filled with black granular material. Albumen gland a large, single-chambered diverticulum.

Penis large, elongate, gradually tapering, occasionally lightly recurved, pigmented uniform black. Penial vas deferens as well-developed duct, semi-closed by epithelium with interlocking, lateral ridges (Fig. 5A). Cephalic vas deferens well developed. Prostate small, posteriorly open to mantle cavity. Seminal vesicles brown, well developed, occupying large surface area. Testis orange.

Right accessory salivary gland poorly developed, very small, somewhat club-shaped. Left accessory salivary gland absent. Paired salivary glands large, located on left and right sides of valve of Leiblein. Salivary ducts attached to anterior portion of esophagus at base of valve of Leiblein. Valve of Leiblein elongate, adjacent to nerve ring. Portion of mid-esophagus with glandular folds short; folds very well developed, wedged into most anterior fold of spiral gland of Leiblein. Gland of Leiblein long, spiral, forming two folds, long, of hard consistency, with thick strawlike external membrane. Duct between mid-esophagus and gland of Leiblein short, poorly developed. Posterior blind duct of gland of Leiblein long, more than half as long as gland of Leiblein, and with terminal ampulla located in dorsal branch of afferent renal vein.

Stomach with large, triangular posterior mixing area, with many small folds oriented towards stomach center. Stomach typhlosole poorly developed, intestinal typhlosole thin. Two digestive diverticula present. Rectum large, embedded in grey opaque connective tissue. Anal opening small but distinct with small papilla, about equal to size of opening and occasionally partially closing it.

Radula: Ribbon length about 20–25% of shell height (Fig. 24E). Rachidian with thin central cusp; small lateral denticle separate from base of lateral cusps; inner edge of lateral cusps smooth, convex; outer edge concave, with faint, small folds at base, and deeply sloping towards edge of rachidian tooth. Lateral teeth long, curved, thin, smooth, simple, about equal in length to rachidian width.

Egg Capsules: Large, elongate, vase-shaped, about 16 mm in height, with concave and convex sides. One suture along lateral edges and continuing across flattened or concave apical plate but interrupted by small, oval, transparent exit hole in center. Between 1,300 and 1,500 embryos per capsule, hatching as veligers (D'Asaro, 1986).

Rapana rapiformis (Born, 1778)
(Fig. 25A–F)

Shell: Protoconch (Fig. 25B) tall, conical, of 3–3.25 adpressed whorls, with minute subsutural plicae and microscopic pustules on last whorls, and with outward-flaring lip and sinusigeral notch. Teleoconch (Fig. 25A) very wide, bulbous, of 7–8 whorls, with canaliculate suture, and with moderately long, wide siphonal canal. Adult shell up to about 125 mm in height, 100 mm in width. Body whorl bulbose, about 90% of shell height (siphonal canal included), sculptured with fine, spiral grooves and with three spiral rows of low, aligned, blunt, partially open knobs; lower two rows of knobs weaker than upper two or absent. Apertural opening very wide, oval, about 80–85% of shell height. Apertural lip semicircular, thin, with faint riblets extending inward, corresponding to external groove pattern. Anterior siphonal canal moderately long, wide, deep, open, about 20% of shell height; posterior siphonal canal poorly developed or absent. Columella rounded and slightly concave, with little callus deposition. Siphonal fasciole composed of partially overlapping distal ends of siphonal canals from previous growth stages. Shell with cream to brown spirally and/or axially continuous or discontinuous bands or blotches; columella and interior of aperture white to orange.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (20–25%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–25%); calcitic layer (10–15%) (Fig. 25D).

Operculum: Inverted tear-shaped, with lateral nucleus in lower right (Fig. 1B). Free surface with staff-shaped growth lines; attached surface with about 3–4 bracket-shaped growth lines and with callused, dull rim (about 35% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot, including long cephalic tentacles and anterior siphon, dark brown to black. Mantle edge simple, straight, following aperture contour, or irregular; anterior siphon extending slightly beyond mantle edge. Accessory boring organ (Fig. 25F, abo), large, dorsal to well-developed pedal gland in females (Fig. 25F, pg).

Osphradial length slightly less than one-half ctenidial length; osphradium and ctenidium equal in width or osphradial width slightly more than ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes, occasionally with posterior portion more tapered. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium bending slightly towards osphradium and extending slightly farther anteriorly than osphradium. Anterior ctenidial lamellae much wider than deep; posterior lamellae about as deep as wide. Lateral and ventral edges of lamellae varying from straight to slightly concave. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vagina large, situated on distal end of partially detached tubular extension of pallial gonoduct and located below and slightly anterior to anal opening. Bursa copulatrix as dorso-ventral slit, continuous with ventral channel and capsule gland. Ventral flange in anterior portion of capsule gland large, curved, originating from ventral epithelium, located under small ventral lobe; flange becoming more reduced posteriorly, located under left and right lobe. Albumen gland omega-shaped with seminal receptacles on dorsal and anterior periphery.

Penis large, strongly recurved, with short, flagelliform tip. Penial vas deferens as duct-within-a-duct system occupying about one-fourth of penial width. Cephalic vas deferens poorly developed. Prostate small, orange, with no obvious duct. Seminal vesicles well developed, pale yellow to golden orange. Testis yellowish.

Proboscis large, brown, equal in width to gland of Leiblein. Paired accessory salivary glands about one-third to one-half of shell height; right gland located on right anterior side of buccal cavity separate from right salivary gland, left one sometimes much smaller

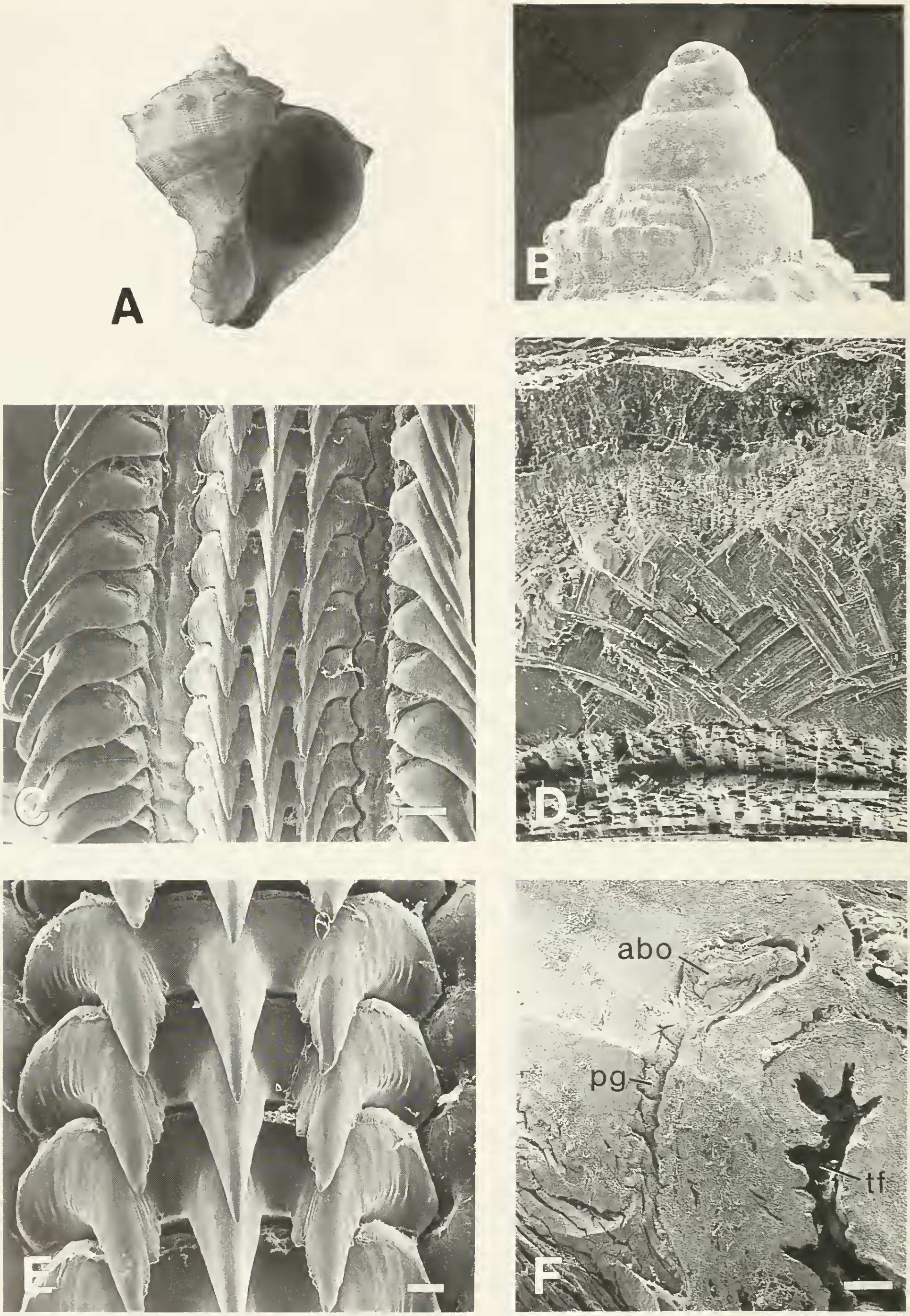

FIG. 25. *Rapana rapiformis*. A, shell (63 mm), apertural view. B, protoconch, side view, SEM (bar = 0.20 mm). C, radula, SEM (bar = 0.10 mm). D, shell ultrastructure, SEM (bar = 75 μm). E, radula, rachidian row, SEM (bar = 30 μm). F, sagittal cross section through anterior foot of female viewed from right side, showing accessory boring organ (abo), ventral pedal gland (pg), and transverse furrow (tf), SEM (bar = 0.50 mm).

than right and embedded in left salivary gland. Salivary glands separate, large; right gland ventral to right side of proboscis, left one adjacent to anterior side of gland of Leiblein and posterior proboscis. Salivary ducts attached at varying distance from valve of Leiblein. Valve of Leiblein short, surrounded by salivary glands, and adjacent to nerve ring. Portion of mid-esophagus with glandular folds long. Duct between esophagus and gland of Leiblein thin, poorly developed. Gland of Leiblein spiral, of hard consistency, large, usually with external strawlike membrane (thickest in older specimens). Posterior blind duct longer than gland of Leiblein itself.

Stomach with large posterior mixing area extending far posteriorly. Five to fifteen folds of different sizes on stomach wall. Stomach typhlosole very well developed, partially extending posteriorly. Intestinal typhlosole narrow and poorly developed. Several thin folds in intestinal groove. Two digestive diverticula present. Rectum large in diameter, thin-walled. Rectal gland not apparent. Anal opening wide.

Radula: Rachidian with thin central cusp (Fig. 25C, E); lateral cusps nearly equal in length to central cusp, with serrated edges; outside of lateral cusp steeply sloping down to edge of rachidian. Lateral teeth broad at base, simple, smooth, about as long as rachidian width.

Egg Capsules: Unknown.

Forreria belcheri (Hinds, 1844)
(Fig. 26A–F)

Shell: Protoconch (Fig. 26B, C) tall, conical, of about two smooth whorls, and with impressed suture; transition with teleoconch smooth. Teleoconch (Fig. 26A) very large, wide, elongate, fusiform, of 6–7 whorls, and with slightly impressed suture. Adult shell up to about 150 mm in height, 95 mm in width, and with long, well-developed siphonal canal. Body whorl (siphonal canal included) about 85% of shell height, with 10–11 varices overhanging new growth; body whorl sculptured with axial growth lines. Large, spinelike knobs on upper corner of square shoulder; moderately deep, wide canal below lower angle of shoulder. Apertural opening wide, oval, about 75% of shell height (siphonal canal included). Apertural lip semi-circular, or semi-hexagonal, thin (even where enforced by varix) to moderately thick; pronounced labial spine on lower lip; interior of aperture smooth and shiny. Anterior siphonal canal long (about 25% of shell height), wide, deep, straight, open; posterior siphonal canal absent. Columella round, moderately curved, with narrow parietal region; moderate callus layer partially detached at margin. Siphonal fasciole well developed, spiny in appearance due to earlier anterior siphonal canals. Wide, concave surface forming umbilicus between siphonal canal (opening) and margin of siphonal fasciole. Shell with faint bands of cream to light brown; columella, interior of aperture and anterior siphonal canal white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (5–10%); aragonitic layer with crystal planes oriented parallel to growing edge (10–20%); calcitic layer (70–80%) (Figure 26F).

Operculum: D-shaped, upper end rounded, with lateral nucleus in lower right (Fig. 1D). Free surface with staff-shaped, growth lines; attached surface with about 7–10 arch- and bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot, including sole, and short, cephalic tentacles greyish. Mantle edge folded. Anterior siphon not extending beyond mantle edge. Accessory boring organ adjacent to pedal gland in females (Fig. 4A). Digestive gland dark brown.

Osphradial length one-fourth to one-third ctenidial length; osphradial width less than one-third ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes, occasionally wider anteriorly, and occasionally with right pectin occasionally slightly wider than left one. Osphradial lamellae attached along varying portions of their base.

Anteriormost portion of ctenidium straight, extending farther anteriorly than osphradium. Anterior and posterior lamellae more than twice as wide as deep (widest and shallowest lamellae located anteriorly). Lateral and ventral edge of ctenidial lamellae varying from straight to concave.

Vaginal opening large, simple, formed from mantle and tubular anterior portion of pallial gonoduct and located below and slightly posterior to anal opening. Bursa copulatrix as

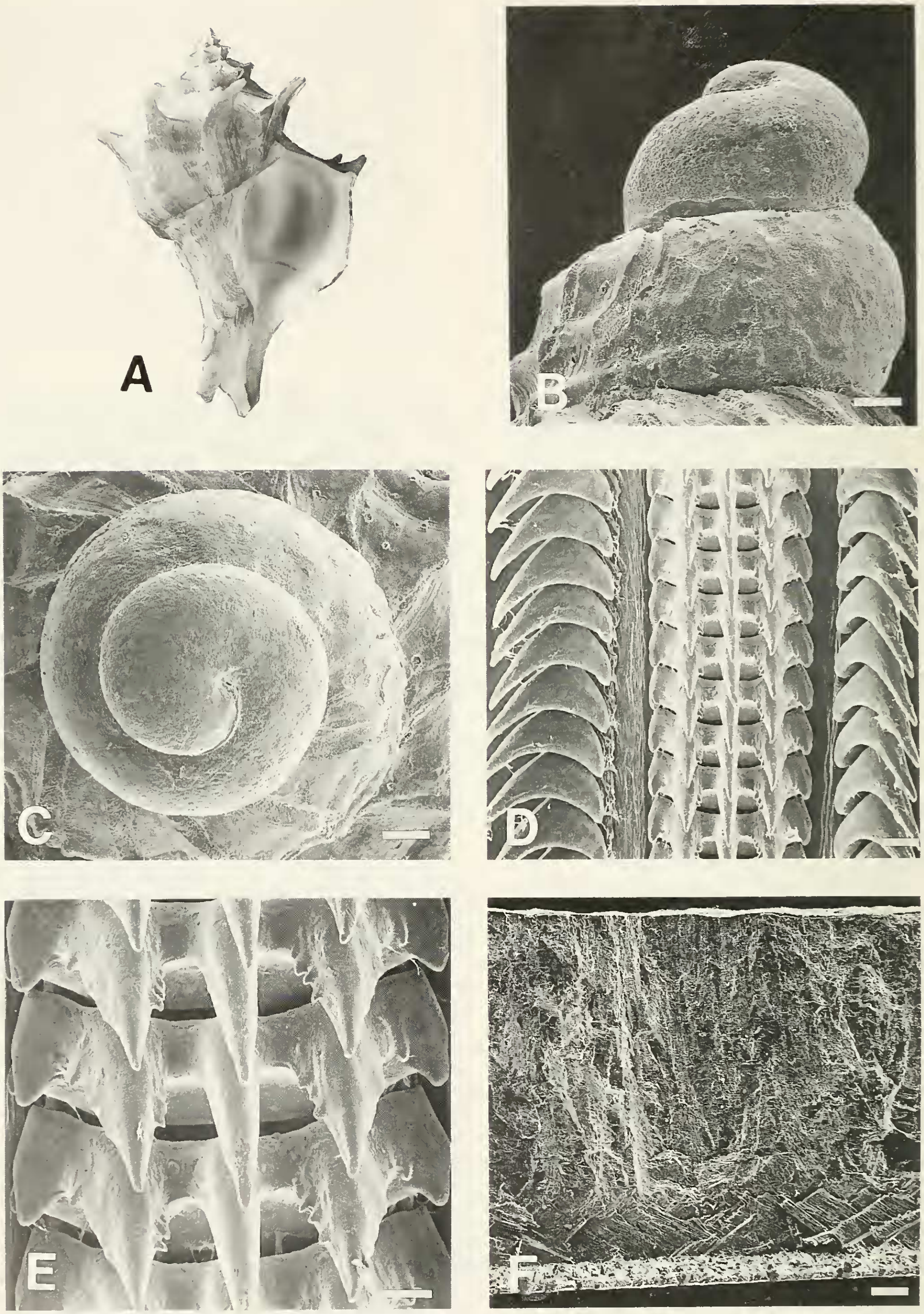

FIG. 26. *Forreria belcheri.* A, shell (114 mm), apertural view. B, protoconch, side view, SEM (bar = 80 µm). C, protoconch, apical view, SEM (bar = 80 µm). D, radula, SEM (bar = 50 µm). E, radula, rachidian row, SEM (bar = 25 µm). F, shell ultrastructure, SEM (bar = 0.10 mm).

large, separate diverticulum. Ventral channel formed by very small flange originating from left capsule gland lobe. Ventral lobe present only in anterior portion of capsule gland. Ingesting gland partially to right of posterior portion of capsule gland, consisting of one large and many smaller chambers, all filled with dark brown granular material. Albumen gland arch-shaped, nearly square in side view, lower ends slightly invaginated. Ovary beige to orange.

Penis elongate, gradually tapering, with microscopic pustules on dorsal side. Penial vas deferens as well-developed duct, semi-closed by epithelium with small, lateral interlocking ridges (Fig. 5A). Cephalic vas deferens well developed. Prostate large, grey to orange brown, composed of two lobes with yellowish longitudinal ridges, and with duct as dorsoventral slit, open ventrally to mantle cavity.

Paired accessory salivary glands extremely long, about one-half of shell height; right gland separate from salivary gland, left gland intertwined with salivary gland. Salivary glands adjacent to left side of proboscis and equal in size to accessory salivary glands. Salivary ducts attached to anterior portion of esophagus at short distance from valve of Leiblein. Valve of Leiblein elongate, with cap structure on anterior end, and surrounded by salivary gland lobes and lying adjacent to nerve ring. Portion of mid-esophagus with glandular folds short; folds very well developed, directly attached to gland of Leiblein. Gland of Leiblein large, spiral, elongate, of hard consistency, lacking strawlike membrane. Posterior esophagus horseshoe-shaped, lying against left side of gland of Leiblein. Posterior blind duct of gland of Leiblein short, less than one-half length of gland of Leiblein.

Stomach with large posterior mixing area and many fine folds oriented towards center of stomach. Small smooth area prior to intestinal area. Stomach typhlosole well developed, intestinal typhlosole thin. Two digestive diverticula present. Rectum moderately wide. Anal opening very small. Anal papilla occasionally formed from anteriorly extended dorsal wall of rectum.

Radula: Ribbon length about 15% of shell height (Fig. 26D, E). Rachidian with thin, needle-shaped central cusp; lateral cusps with 3–4 inner denticles and serrated outer edge with 1–2 faint outer denticles on base; base of outer edge of lateral cusps adjacent to base of inner edge of large marginal cusp; marginal cusps in different plane than lateral cusps (about 75° angle) and parallel to elongate lateral extension at base of rachidian tooth, resulting in bifid rachidian edge (compare Fig. 15E). Lateral teeth broad, smooth, simple, equal in length to rachidian width.

Descriptions of Taxa Used to Test Robustness of Synapomorphies

The species *Acanthina monodon* and *Trochia cingulata* were only examined on few features after initial cladistic analyses had revealed synapomorphies for a clade consisting of *Nucella* and *Forreria.* These two species, suspected of being closely allied to *Nucella* and *Forreria,* were tested for having the same synapomorphies as found for the *Nucella-Forreria* clade. The two taxa were usually included in Thaididae/nae of authors.

Acanthina monodon (Pallas, 1774)
(Fig. 27A–D)

Anatomical data for *Acanthina monodon* were obtained from Wu (1985); this species has a bursa copulatrix that is separate from the lumen of the capsule gland, very long accessory salivary glands, a lightly curved penis with pseudo-papilla, an accessory boring organ separate from the ventral pedal gland (in females; Fig. 4A), and a D-shaped operculum with its upper end rounded and with a lateral nucleus in the lower right (compare Fig. 1D). Scanning electron micrographs of the shell ultrastructure were not available at the time of the cladistic analysis, but from light microscopy it was obvious that an inner aragonitic layer with the crystal planes oriented in a 45° angle to the growing edge is absent. The protoconch (Fig. 27C, D) is smooth, paucispiral (about 1.5 whorls), and lacks an outward-flaring lip.

Trochia cingulata (Linnaeus, 1758)
(Fig. 28A–E)

Scanning electron micrographs of the protoconch and the shell ultrastructure revealed a smooth, paucispiral protoconch of about 1.5 whorls, lacking an outward-flaring lip (Fig. 28C, D), and a shell ultrastructure consisting of an aragonitic layer with crystal planes oriented perpendicular to growing edge (10–30%), an aragonitic layer with crystal planes oriented parallel to growing edge (25–

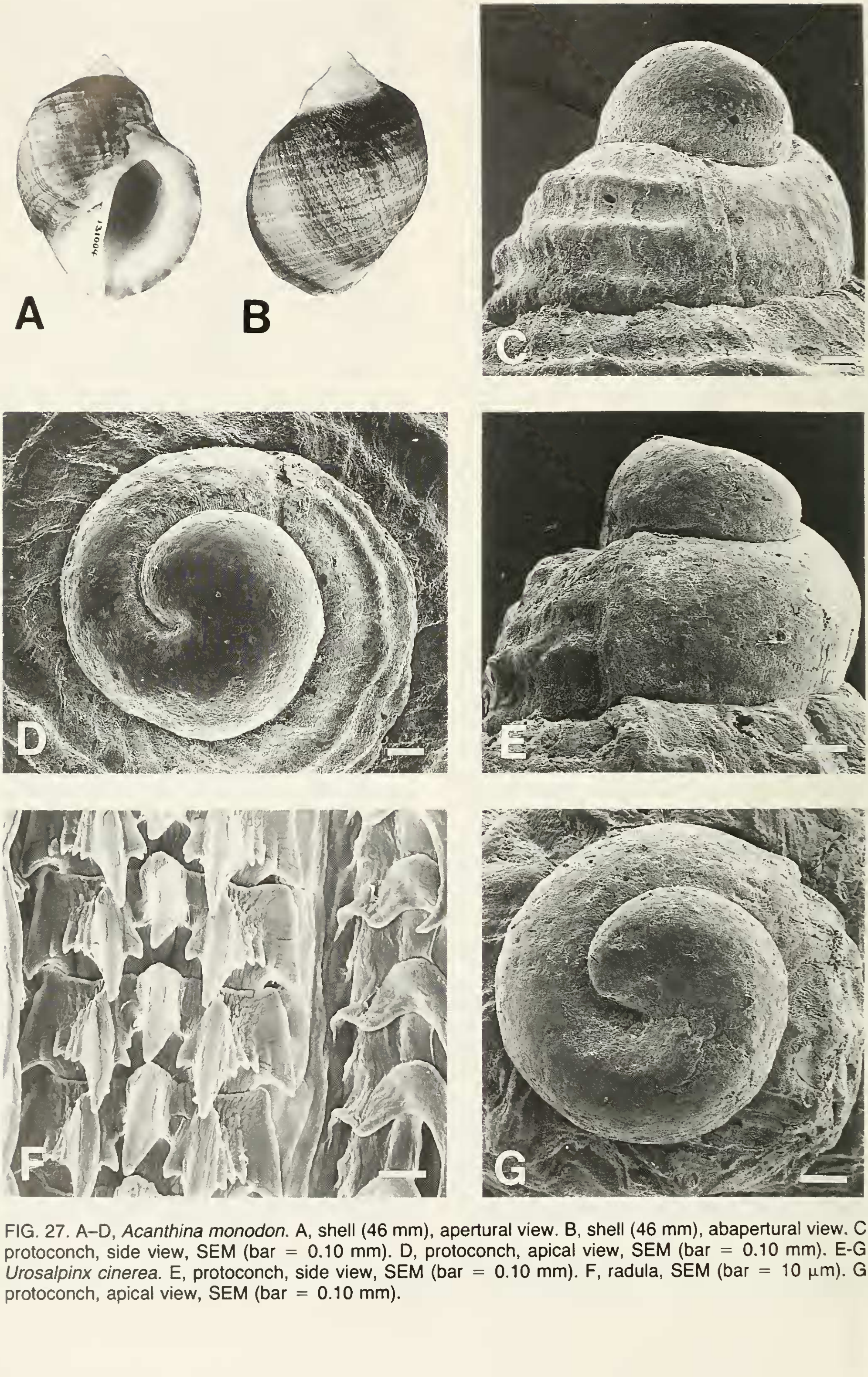

FIG. 27. A–D, *Acanthina monodon*. A, shell (46 mm), apertural view. B, shell (46 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E-G, *Urosalpinx cinerea*. E, protoconch, side view, SEM (bar = 0.10 mm). F, radula, SEM (bar = 10 μm). G, protoconch, apical view, SEM (bar = 0.10 mm).

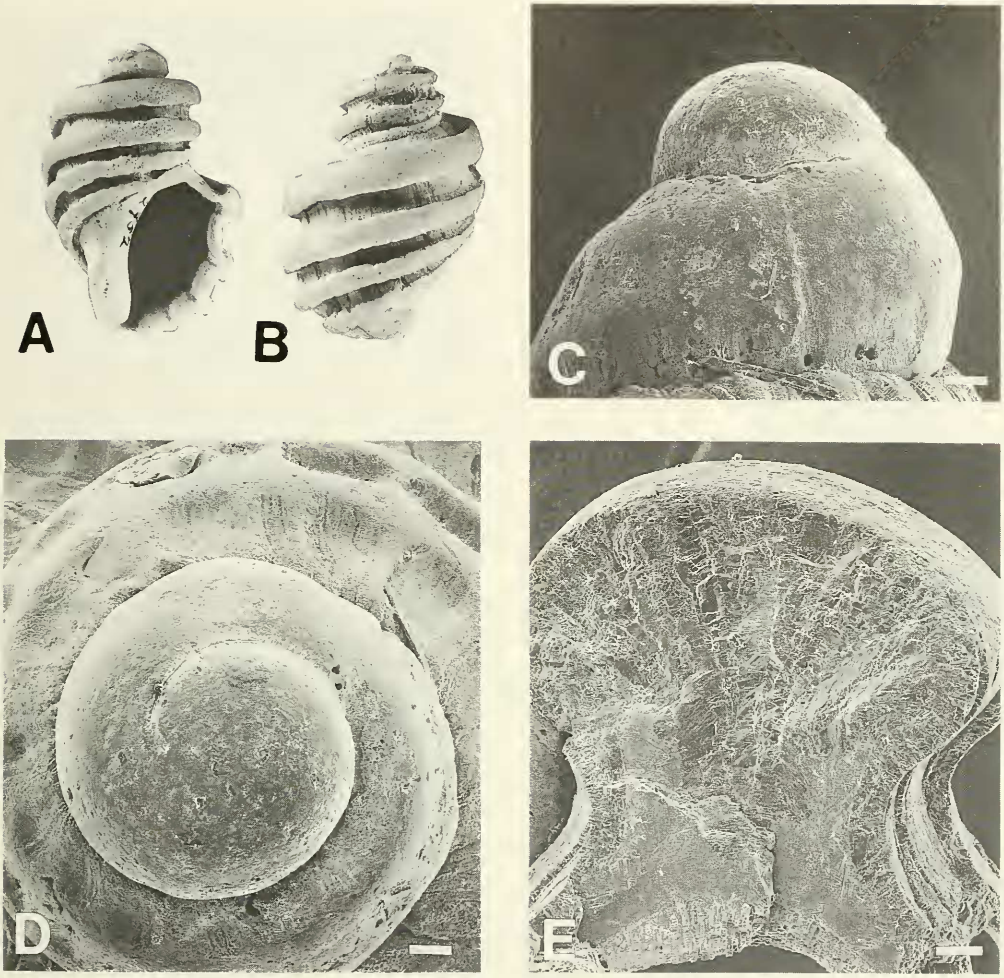

FIG. 28. *Trochia cingulata*. A, shell (40 mm), apertural view. B, shell (40 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, SEM (bar = 50 μm).

40%), and a calcitic layer (30–65%) (Fig. 28E).

Phylogenetic Analysis

Figure 30 shows a consensus tree of 6,288 trees obtained with all multistate characters (Table 3) scored as unordered and using the rigorous "mh* bb*" command. The consistency index of each of the trees is 0.86; the consistency index of the consensus tree is 0.77.

DISCUSSION AND CONCLUSIONS

Phylogenetic Analysis

It is obvious that the Thaididae/nae of authors, which prior to now usually included all taxa used in this study except *Muricanthus, Rapana,* and (usually) *Forreria,* can be divided into two monophyletic groups and that para- and polyphyly was present in previous taxonomic arrangements both at the generic and (sub)familial levels. For example, the type species of *Nucella* (often referred to in the literature as "*Thais*" *lapillus* or "*Purpura*"

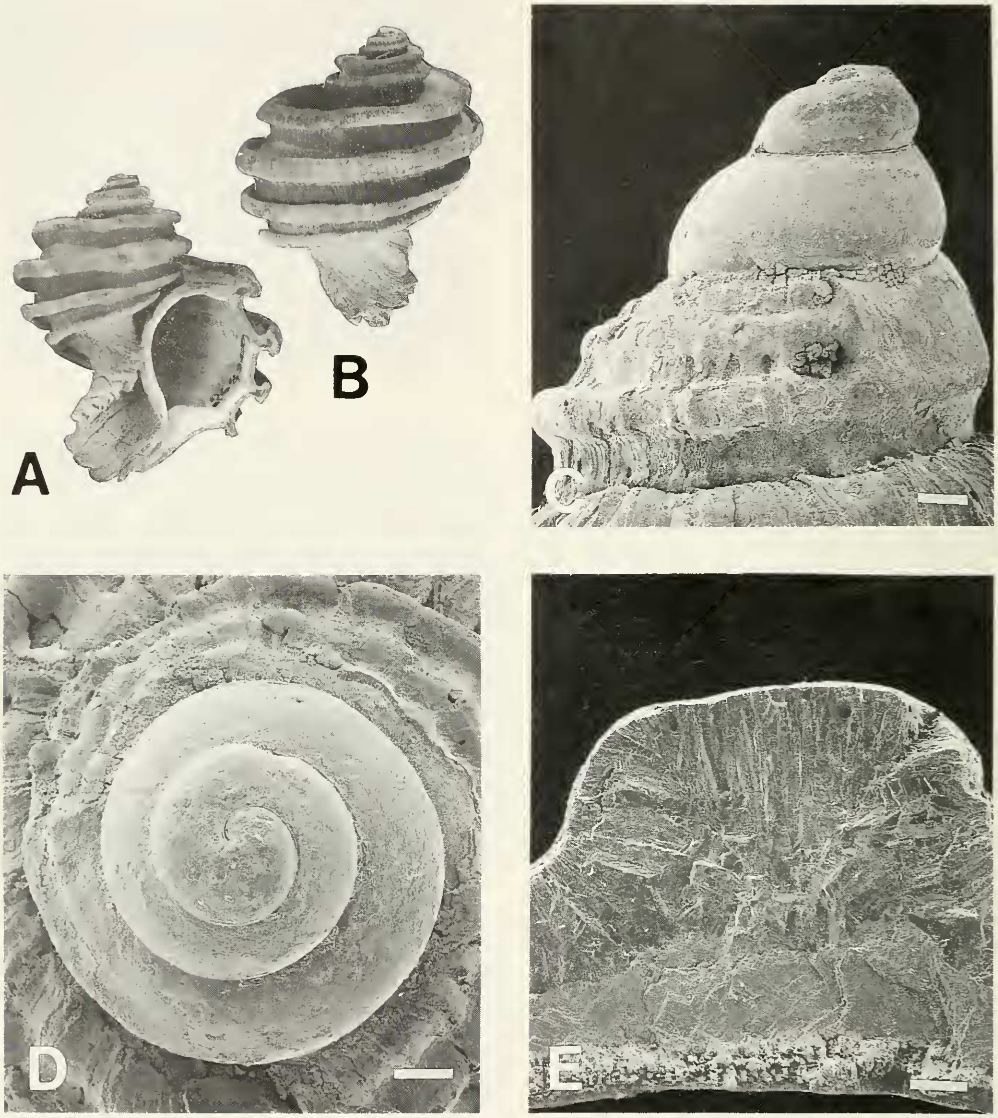

FIG. 29. *Ecphora* cf. *quadricostata*. A, shell (71 mm), apertural view. B, shell (71 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.15 mm). D, protoconch, apical view, SEM (bar = 0.15 mm). E, shell ultrastructure, SEM (bar = 0.30 mm).

lapillus), is excluded from the taxon name to be used for Clade C (Fig. 30), based on a wide variety of characters, many of which it shares as synapomorphies with *Forreria belcheri,* the type species of *Forreria,* which was previously grouped within the Rapaninae as well as Thaidinae.

The high number of trees is partially due to the lack of data for two of the species of Clade B (*Acanthina monodon* and *Trochia cingulata*). This resulted in a multitude of resolutions for this clade and thus increased the total number of equally parsimonious trees.

The number of convergences and parallelisms among the two main clades (e.g. a separate pedal gland and accessory boring organ in *Nucella* and *Cymia*) and the outgroup, indicate that boundaries among these three

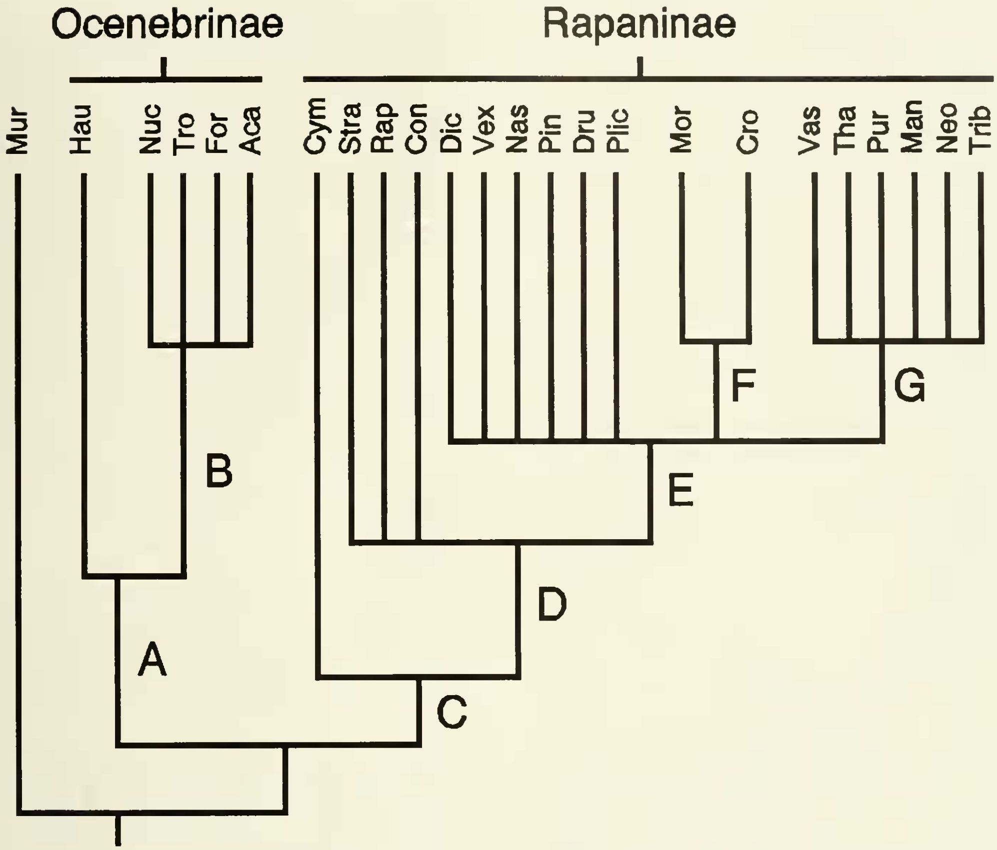

FIG. 30. Consensus cladogram with taxonomic groupings superimposed. Mur = *Muricanthus;* Hau = *Haustrum;* Nuc = *Nucella;* Tro = *Trochia;* For = *Forreria;* Aca = *Acanthina;* Cym = *Cymia;* Stra = *Stramonita;* Rap = *Rapana;* Con = *Concholepas;* Dic = *Dicathais;* Vex = *Vexilla;* Nas = *Nassa;* Pin = *Pinaxia;* Dru = *Drupa;* Plic = *Plicopurpura;* Mor = *Morula;* Cro = *Cronia;* Vas = *Vasula;* Tha = *Thais;* Pur = *Purpura;* Man = *Mancinella;* Neo = *Neorapana;* Trib = *Tribulus.*

groups are not sufficiently clear-cut to justify familial ranking for all three clades. I suggest that these clades merely be ranked as subfamilies.

The taxa on Clade A form a distinct, cohesive clade, despite the limited data available for two of its taxa. Previously, the genera *Haustrum, Acanthina, Nucella, Trochia,* and *Forreria,* had been included in Thaididae/nae of authors, although *Forreria* has also been allocated to Rapaninae of authors. However, the five species in Clade B show no more resemblance with members of Clade C than they do with *Muricanthus* (Muricinae). As stated earlier, studies of *Ocenebra s.s.* (Kool, 1993) revealed close phylogenetic relationship among Ocenebrinae and the taxa of Clade A.

The consensus tree shows that including only *Rapana* in Rapaninae would result in paraphyly. *Cymia* can be considered as an atypical member of Rapaninae (see below), but providing it with separate subfamilial status appears unjustified. All taxa of Clade C should be included in Rapaninae. Perhaps future studies will reveal that Rapaninae should be further subdivided into two or more subfamilies. For example, in some previous analyses *Cronia* and *Morula* grouped at the base of Clade C (Kool, 1989); either these two genera are very highly derived members of Clade C, or their placement in Clade C should be subjected to further examination, which may show that they are better placed in Ergalataxinae Kuroda & Habe, 1971. The present study, however, indicates that all taxa of

TABLE 3. Characters and character states. Numbers and letters correspond to those in text.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Taxon																		
Muricanthus	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Forreria	b	b	b	a	b	a	b	a	a	a	b	a	a	a	b	?	b	c
Nucella	b	b	b	a	b	a	b	a	a	a	b	b	c	a	b	b	b	c
Haustrum	b	?	c	a	b	a	a	a	a	a	b	b	b	a	e	b	a	b
Morula	a	a	a	a	c	b	a	b	b	b	c	c	d	b	c	a	a	e
Cronia	c	a	a	a	c	b	a	b	b	b	d	c	d	b	c	a	a	e
Rapana	a	a	c	a	d	a	a	a	b	c	d	e	d	b	b	a	a	f
Cymia	?	?	c	a	e	a	b	a	b	a	?	d	d	b	b	a	a	d
Stramonita	a	a	b	a	e	a	a	a	b	c	d	e	d	b	b	a	a	g
Concholepas	a	a	b	a	e	a	a	a	b	c	d	e	d	b	b	a	a	g
Dicathais	c	a	b	a	e	a	a	b	b	c	?	e	d	b	c	a	a	g
Vasula	?	?	?	b	e	a	a	b	b	c	d	e	d	b	c	?	a	j
Vexilla	d	a	a	a	f	a	c	b	b	c	d	f	d	b	d	a	a	?
Nassa	a	a	a	a	e	a	a	b	b	c	d	f	d	b	c	a	a	?
Pinaxia	a	a	a	a	e	a	a	b	b	c	d	f	d	b	c	a	a	h
Drupa	?	?	?	a	e	a	a	b	b	c	d	e	d	b	d	a	a	h
Plicopurpura	a	a	?	a	e	a	a	b	b	c	d	e	d	b	c	a	a	?
Thais	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	j
Purpura	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	h
Mancinella	?	?	c	b	e	a	a	b	b	c	?	e	d	b	c	a	a	i
Neorapana	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	j
Tribulus	?	a	c	b	e	?	a	b	?	?	?	e	d	?	?	?	a	j
Acanthina	b	b	?	a	b	?	b	?	a	?	?	b	?	?	?	?	?	?
Trochia	b	b	b	a	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Clade C are to be included in one subfamily, of which *Rapana* is the provider of the subfamilial name. Thaidinae becomes a subjective junior synonym of Rapaninae, by priority.

A discussion of the relationships among the taxa of the main clades of the consensus cladogram (Fig. 30) follows.

Clade A: Haustrum haustorium is more reclosely allied with the species of Clade B than it is with any of the species of Clade C. Two of the taxa of Clade B (*Acanthina* and *Trochia*) were not examined in detail for this study, but they grouped unambiguously with *Nucella* and *Forreria* based on the data available. Nevertheless, the hiatus of character states of these two taxa resulted in a large number of variations in the resolution of Clade B, contributing to the high number of trees obtained from the analysis.

Clade C (individual clades treated separately): Although *Cymia* is included in Clade C, it shares a synapomorphy with the species of Clade B (accessory boring organ and ventral pedal gland [females] with separate duct) and lacks, as do all members of Clade A, a synapomorphy found in all other members of Clade B (posterior seminal receptacles [females]). However, *Cymia* shares several synapomorphies with all other taxa of Clade B (bursa copulatrix continuous with capsule gland [females], strongly recurved penis, closed prostate, penial vas deferens a duct-within-a-duct [males]). Further detailed studies may determine whether the placement of this atypical, perhaps primitive, species in Rapaninae is justified.

The radular morphology of *Cymia tecta* reveals a possibly closer relationship with *Haustrum* than the tree topology indicates. To *a posteriori* test for homology (Patterson, 1982) in the radular morphology, the radular characters (17 and 18, Table 3) of *Cymia* were alternatively scored identical to those in *Haustrum,* because the superficial resemblance may be indicative of homology. However, this did not alter the tree topology; other characters overrode this "attempted" switch of *Cymia* to Clade A, and the original placement prevailed.

Clades D, E, F, G: Clades D and E have suffered significant loss of resolution compared to the individual trees from which the consensus tree was obtained. However, several distinct and stable clades can be found higher up the tree. Clade G consists of the taxa *Vasula, Thais, Purpura, Mancinella, Neorapana,* and

Tribulus. The similarity in radular morphology among the taxa *Thais, Tribulus, Neorapana,* and *Vasula* suggests that at these four genera are only distinct at the subgeneric level; I consider *Tribulus, Neorapana,* and *Vasula* subgenera of *Thais,* the oldest available name. *Mancinella* and *Purpura* are sufficiently different in radular morphology from one another and from the other four genera in Clade G to justify separate generic status for these two taxa. This separation at the generic level is further supported by the topologies of many of the obtained trees. Clade F, consisting of *Morula* and *Cronia,* is also very stable.

The low resolution among the taxa *Rapana, Stramonita,* and *Concholepas* of Clade D, and of *Dicathais, Vexilla, Nassa, Pinaxia, Drupa,* and *Plicopurpura* of Clade E, can be attributed to several factors. The characters and character states used are adequate to identify major groups, but are not sufficiently robust to yield only one most parsimonious, highly resolved tree. At the lower taxonomic levels, convergence and parallelism appear to be more common, thus increasing the number of equally parsimonious branching patterns. This low resolution could furthermore be attributed to close phylogenetic relationship. I propose that a combination of these factors is the cause for a low resolution in Clades D and E, as well as in Clades B and G. It should be noted that low resolution by itself does not provide a strong argument for synonymization of any of the genera in these clades; autapomorphies for the type species of a genus most likely become synapomorphies for almost all species within that genus when more species are added to the analysis.

Character State Transformations on Cladogram

The topology of the cladogram (Fig. 30) supports a single hypothesis for character-state evolution in 13 characters. More than one (and equally parsimonious) transformation series are possible for the remaining five (3, 5, 11, 12, and 18). I chose for the scheme which would place character-state changes as high on the tree as possible; this reasoning prevents placement of less informative synapomorphies to be placed in basal positions. For example, if state (a) occurred in the outgroup, (b) in Clade A (Fig. 30), and (c) in Clade C, I would choose a scheme whereby both (b) and (c) evolved from (a), although it would be equally parsimonious to assume a linear transformation series [(a) → (b) → (c) or (a) → (c) → (b)].

The hypotheses about character state evolution and possible causal schemes are discussed below. The numbers and letters assigned to, respectively, the characters and character states correspond to the numbers and letters in Table 3 and to those in the list of characters in MATERIALS AND METHODS.

Protoconch:—Number of whorls and sculpture (1). From a multispiral, sculptured condition (a) (e.g. Fig. 24C) evolved three other conditions: a paucispiral, smooth condition (b) (e.g. Fig. 15C); a multispiral, smooth condition (c) (e.g. Fig. 9C); and a paucispiral, sculptured condition (d) (e.g. Fig. 23D).

—Transition into teleoconch (2). The apomorphic condition is the absence of an outward-flaring lip and sinusigeral notch (b) (e.g. Fig. 15C). In most of the studied taxa, these features are present (a) (e.g. Fig. 13D). The absence of the outward-flaring lip and sinusigeral notch correlates with the mode of development; species with direct development lack these features, whereas it is present in taxa with a planktonic larval stage. The tree topology suggests that the direct mode of development evolved from a free-swimming mode of development.

Shell Ultrastructure:—Calcitic outer layer (3). Absence of calcite is the plesiomorphic condition (a); presence of calcite is the derived condition. The presence of calcite is arbitrarily quantified into the states "thick" (> 25% of total shell thickness) (b) (e.g. Fig. 15G), and "thin" (< 20% of total shell thickness) (c) (e.g. Fig. 20E). A thick layer probably evolved from a thin layer.

It is difficult to determine whether calcite is present in *Drupa, Vasula* and *Plicopurpura.* Crystallographic (e.g. X-ray diffraction) techniques should be used to determine whether calcite is present in those taxa scored with "?" for this character in Table 3. The lacking data and low resolution of the cladogram does not allow for speculation on evolutionary trends for this character, other than that the lack of calcite is the plesiomorphic condition found in the outgroup, some members of the Rapaninae, and in other neogastropods (Buccinidae, Volutidae, etc.) (Harasewych & Kool, in preparation).

—45° innermost aragonitic layer (4). Absence of this inner layer of aragonite, the crystal planes of which are oriented in a 45°

angle to the growing edge, is the plesiomorphic condition (a); presence of this layer is the derived state (b) (e.g. Fig. 20E). This layer not only adds thickness to the shell, but presumably also gives more strength to it, which may serve as defense to predation.

Operculum:—Morphology of operculum (5). The opercular shape in the outgroup is oval, with a terminal nucleus in the lower right, and with concentric growth lines (a) (Fig. 1A). This condition gave rise to both a D-shaped operculum with upper end rounded and with lateral nucleus in the lower right (b) (e.g. Fig. 1D), and a D-shaped operculum with a lateral nucleus in the center right (e) (e.g. Fig. 1C). From this last condition (e) arose three other opercular morphologies: an inverted tear-shaped operculum with a rounded upper edge, a tapered lower end, and with a lateral nucleus in the lower right (d) (e.g. Fig. 1B); a D-shaped operculum, tapered at the lower end, with an S-shaped left edge (adjacent to columella), and with a lateral nucleus in the lower right (c) (e.g. Fig. 1F); and an ovate-elongate operculum, tapered at the lower end, and with a lateral nucleus in the upper right (f) (Fig. 1E).

The shape of the operculum is, of course, largely dependent on aperture shape; however, it is interesting that the operculum of *Haustrum,* a non-rapanine, is very different in morphology from that of *Purpura* or *Plicopurpura,* whereas these three species have extremely similar apertural shapes. It should be noted that the operculum of *Rapana rapiformis* is scored differently from the other rapanines, but that the operculum of other *Rapana* species is D-shaped and with a nucleus in the center right, as in most other rapanines.

Taki (1950) provided an evolutionary scenario for opercular morphologies in which a D-shaped operculum with an "extranuclear" nucleus (as found in *Purpura*) evolved from an ovate operculum with an "extraeccentric" nucleus (as found in *Muricanthus*).

—Rodlike structures in hypobranchial gland (6). Presence of rodlike structures in the hypobranchial gland, oriented perpendicular to the mantle (b) is the apomorphic condition (Fig. 2A, B). The function of these structures is not known.

—Ventral pedal gland and accessory boring organ (7). In female specimens of the outgroup and in many of the rapanines, the accessory boring organ and ventral pedal gland share a common duct to the outside (a) (Fig. 4B). From this condition arose two conditions: the development of a ventral pedal gland with an opening separate from that of the accessory boring organ (b) (Fig. 4A); and loss of the accessory boring organ (c).

In the majority of taxa studied herein, a single accessory boring organ duct is responsible for the excretion of decalcifying agents and for the intake and tanning of egg capsules. The derived condition of having separate ducts enables the female to specialize both structures further and may allow feeding during periods between laying eggs. This increase in flexibility is of more importance to snails with seasonal patterns in feeding and spawning, than to those that can feed and spawn at any time. The most derived condition is loss of the accessory boring organ, which probably is the result of specialized feeding habits. (*Vexilla* is parasitic on urchins [Kay, 1979; Kool, 1987].)

Mantle Cavity Organs:—Osphradial length relative to ctenidial length (8). The plesiomorphic condition is an osphradial length of less than one-half the ctenidial length (a). This condition gave rise to an osphradial length of at least one-half that of the ctenidium (b) (Fig. 3D).

Numbers of osphradial lamellae vary from about 7–14 per mm; those of the ctenidium from 9–22 per mm. It seems probable that a relatively larger osphradium facilitates the search for food. However, because the osphradium is measured against ctenidium size, it may be that the small size of the ctenidium only causes the osphradium to appear larger than the osphradium in other species. Furthermore, the density of osphradial lamellae may be age and/or size dependent. This character thus does not lend itself for adaptationist schemes.

Female Reproductive System:—Bursa copulatrix (9). A sacklike bursa, usually located anterior to the capsule gland, and with its lumen separate from that of the capsule gland is the plesiomorphic condition (a) (Fig. 4C). From this condition evolved a bursa that is merely an anteriorly located specialized extension of the capsule gland (b) (Fig. 4D).

—Posterior seminal receptacles on dorsal periphery of the albumen gland (10). Absence of these structures is the plesiomorphic condition (a) (Fig. 4F, G); from this condition evolved a development of specialized structures for sperm storage that open into the albumen gland (c) (Fig. 4H). A situation where two or three seminal receptacles branch off the ovi-sperm duct appears to have evolved from the latter condition (b) (Fig. 4E).

Kool (1988a, b) described in detail why the posterior seminal receptacles, which open directly into the albumen gland, allow a more efficient mode of fertilization, and suggested that this evolutionary novelty may have triggered a radiation in rapanines. Presence of a specialized receptacle branching off the ovi-sperm duct could be interpreted as an intermediate condition, but the tree topology suggests it is the most highly derived condition.

—Morphology of albumen gland (11). The ancestral condition of albumen gland morphology was most likely a dorsally swollen oviduct, which then developed into a lobular structure (a) (Fig. 4F). Two morphologies evolved from this ancestral state. The ventral side of the oviduct may have invaginated, resulting in an arch-shaped tube, appearing like a tube coiled onto itself (b) (Fig. 4G), and an omega-shaped tube (d) (Fig. 4H). From the last condition (d) arose a more asymmetrical, staff-shaped albumen gland (c) (Fig. 4E).

If, indeed, this is the sequence of evolutionary events in the development in this character, it may be hypothesized that albumen glands became more efficient in the process of coating of albumen due to an increased surface area and a longer route for the eggs to travel (Kool, 1988a, b). Higher efficiency may explain the reduction of the anterior lobe of this gland in a highly derived taxon, such as *Morula*.

Male Reproductive System:—Morphology of penis (12). The outgroup has an elongated, occasionally lightly curved, gradually tapering penis (a) (Fig. 5A). From this shape, several different morphologies evolved: a relatively short, wide, straight or lightly curved penis with a small pseudo-papilla (b) (Fig. 5B); an elongate, wide penis, strongly recurved, club-shaped, with a slightly swollen distal end (d) (Fig. 5F); a consistently strongly recurved penis tapering distally into a flagelliform appendage of varying length (e) (Fig. 5D). From (e) evolved a slightly recurved penis, long and gradually tapering distally (f) (Fig. 5C); the tree topology furthermore suggests that a penis with a large side lobe (c) (Fig. 5E, I, sl) evolved from (e). The side lobe may have some purpose in the copulation process.

—Morphology of penial vas deferens (13). The outgroup has a well-developed duct, semi-closed by interlocking lateral ridges (a) (Fig. 5A). From (a) evolved three states: an open duct, located on the posterior edge of the penis (b); a semi-closed condition, similar to (a), but with minute duct and without lateral ridges, and lying more adjacent to the penial posterior edge (c) (Fig. 5B); and a convoluted, coiling, meandering tube within a larger cavity (duct-within-a-duct system) (d) (Fig. 5D).

Histological studies may show that the dorsal and ventral flaps of tissue in conditions (a) (with lateral ridges) and (c) (without lateral ridges) are held together by cilia. Dissections of well-preserved specimens of *Haustrum* will determine whether the "open" condition is not an artifact of poor preservation.

—Morphology of prostate duct (pallial vas deferens) (14). A prostate duct that is in open connection with the mantle cavity (in the posterior portion) is the plesiomorphic character state (a) (Fig. 5H). A duct closed throughout the prostate developed from this condition (b) (Fig. 5G).

A prostate with a duct in open connection with the mantle cavity may be to some advantage by allowing for an emergency release for sperm in case the snail is forced to withdraw into the shell. However, it is doubtful that the elasticity of the pallial gonoduct could not absorb some extra pressure while the animal is withdrawing. Furthermore, loss of sperm would be prevented in a closed prostate duct.

Alimentary System:—Length of accessory salivary glands (15). A very poorly developed, almost vestigial, minute right accessory salivary gland is present in the outgroup (a). From this condition arose a pair of very long accessory salivary glands (up to over one-half of shell height) (b), from which arose two other conditions: presence of a very well-developed, long (nearly one-half of shell height) right accessory salivary gland (e), and a pair of glands of short to medium length (less than one-fourth of shell height) (c) (Fig. 3F, ra, la). From the latter condition evolved loss of both the left and the right glands (d).

—Length of posterior blind duct of gland of Leiblein (16). The plesiomorphic condition is a long duct ($\geq$ one-half length of gland itself) (Fig. 3F, dgL) which reaches into the dorsal branch of the afferent renal vein (a). From this condition evolved a very short duct ($<$ 1/2 of length of gland itself) which empties into the posterior portion of the cephalic cavity (b) (Fretter & Graham, 1962: fig. 153).

Radula (Rachidian):—Orientation of marginal cusp (17). A marginal cusp in the same plane with the lateral cusp is the plesiomorphic condition (a). From (a) arose a marginal cusp which is in a different plane with the lateral cusps (b) (e.g. Fig. 15E, F).

—Morphology of cusps on rachidian tooth (18). From a rachidian without a marginal area and cusps, with a small, free-standing inner lateral denticle, and long lateral cusps (a) (Fig. 24E) evolved four morphologies; the first, without marginal area and cusps, with large, free-standing inner lateral denticle and long lateral cusps (b) (Fig. 11D); the second, without marginal area, with small marginal cusps, one or more inner lateral denticles and long lateral cusps (c) (e.g. Fig. 15F); the third, without marginal area, with small marginal cusps, a small inner lateral denticle and short, nearly triangular lateral cusps (d) (Fig. 8H); the fourth, without marginal area, with small marginal cusps, with one or more inner lateral denticles and long lateral cusps (g) (e.g. Fig. 7F). From (g) arose four other rachidian morphologies: a wide marginal area, without marginal cusps, with free-standing inner lateral denticle and short lateral cusps (e) (e.g. Fig. 8D); one without marginal area and cusps, with several faint inner lateral denticles and long lateral cusps (f) (Fig. 25C, E); one with wide marginal area with many denticles and a small marginal cusp, a small inner lateral denticle and long lateral cusps (h) (e.g. Fig. 18D); and one with a short marginal area, with small marginal cusps, with or without small inner lateral denticle and with long lateral cusps (j) (e.g. Fig. 22E). From (j) evolved a rachidian without marginal area and cusps, without inner lateral denticles, and with short lateral cusps (i) (Fig. 11I). Three additional morphologies (scored with "?") that arose from (g) are: similar to (i) but with a free-standing lateral denticle in some specimens, and with short lateral cusps (Fig. 13G); also similar to (i), but with slit in central cusp (Fig. 17E); and the last situation, also similar to (i) but with the base of the central cusp nearly as wide as the rachidian itself (Fig. 23C).

The following are synapomorphies for the different clades and taxonomic groups of the consensus tree (Fig. 30).

Clades A, C ("the ingroup"):
(1) layer of calcite of medium thickness (character 3).
(2) accessory salivary glands very long (nearly one-half of shell height) (character 15).

Calcite is absent in several taxa of Clade E, whereas a thick layer of calcite is present in taxa in Clades B and D (see remarks under *Clade G*). Among taxa of both clades, the accessory salivary glands vary from medium in size to absent.

Clade A (Ocenebrinae):
(1) protoconch paucispiral and smooth (Character 1).
(2) operculum D-shaped, with upper end rounded and with lateral nucleus in lower right (character 5).
(3) albumen gland arch-shaped, elongate (character 11).
(4) penis straight or mildly curved with pseudo-papilla (character 12).
(5) short blind duct of gland of Leiblein (character 16).

Clade B (within Ocenebrinae):
(1) transition from protoconch to teleoconch smooth, outward-flaring lip absent (character 2).
(2) layer of calcite thick (character 3).
(3) accessory boring organ separate from pedal gland (character 7).
(4) marginal cusp in different plane than lateral cusp (character 17).
(5) rachidian with small marginal cusps, one or more small inner lateral denticles, and with lateral cusps nearly equal in length to central cusp (character 18).

A thick calcitic layer (2) and separate ducts for the accessory boring organ and ventral pedal gland (3) are also found in Clade C (*Cymia*) and are probably the result of parallel evolution. Absence of an outward-flaring lip (1) may become a synapomorphy for Clade A, once it is shown that the transition from protoconch to teleoconch in *Haustrum haustorium* is smooth.

Clade C (Rapaninae):
(1) operculum D-shaped, with lateral nucleus in center right (character 5).
(2) bursa copulatrix continuous with capsule gland (character 9).
(3) penial vas deferens as duct-within-a-duct (character 13).
(4) prostate gland closed to mantle cavity (character 14).

Clade D:

(1) posterior seminal receptacles on dorsal periphery of albumen gland (character 10).
(2) omega-shaped albumen gland (character 11).
(3) penis strongly recurved, with flagellate pseudo-papilla (character 12).
(4) marginal area absent, marginal cusps small; one or more inner lateral denticles; lateral cusps nearly equal in length to central cusp (character 18).

Clade E:

(1) layer of calcite absent (reversal; see remarks under Clade G) (character 3).
(2) osphradial length at least one-half ctenidial length (character 8).
(3) accessory salivary glands short to medium (character 15).

Clade F:

(1) operculum D-shaped, with tapered lower end, S-shaped left edge, and with lateral nucleus in lower right (character 5).
(2) rodlike structures in the hypobranchial gland (character 6).
(3) 1–3 large seminal receptacles lying over the dorsal periphery of albumen gland, and branching off ovi-sperm duct (character 10).
(4) penis with large side lobe (character 12).
(5) rachidian with very wide, smooth marginal area, without marginal cusps, with small inner lateral denticle free from lateral cusp, and with central cusp much longer than lateral cusps (character 18).

Clade G:

(1) layer of calcite thin (character 3).
(2) innermost aragonitic shell layer with crystal planes oriented in 45° angle to growing edge (character 4).
(3) short marginal area with small marginal cusps; inner lateral denticle small or absent; lateral cusps nearly equal in length to central cusp which is wide at base (character 18).

A thin calcitic layer appears to have evolved in a parallel manner in one taxon in Clade A (*Haustrum*) and in two taxa within Clade C (*Cymia*, *Rapana*). This layer is absent in many taxa of Clade E (reversal as synapomorphy for this Clade) and is present again in the taxa of Clade G. This character-state distribution suggests that this character needs more detailed study and that the pattern of parallelism, convergence and reversal in character 3 may only be the result of inadequate understanding of this character.

Congruence between Proposed Phylogeny and Fossil Record

There are several reasons for not basing a branching sequence on the fossil record of rapanines *a priori*. First, rapanines do not fossilize well in their rocky intertidal environment and have a poor, incomplete fossil record. Thus, an extant taxon with a short fossil history may be part of a primitive lineage with fossil members which have either not yet been discovered or have not been identified as close allies of the extant species.

The second reason for not using the fossil record *a priori* is the problem of taxon identification, especially above the species level, which at most may be based on superficial shell characters. It is difficult to identify phylogenetic relationships among Recent taxa on the basis of external shell morphology alone and even more so to determine phylogeny from fossil shells. For example, because of convergence in shell shape, what may be identified as a fossil species of *Morula* may not be related to Recent *Morula s.s.* species.

Thirdly, fossil records taken from the literature are often unreliable because limits have not been set for most rapanine genera. This causes the scope of genera to vary widely among authors. For example, some of the fossil records of so-called "*Thais s.s.*" may not be based on fossils of the type species of *Thais,* which has a very limited geographical distribution. Rather, they may be based on fossils of the nominal species "*haemastoma,*" which many authors have placed under *Thais*, but is herein shown to belong in the genus *Stramonita.* If *Stramonita* had a longer fossil record than *Thais s.s.,* the geological record of *Thais* would be erroneously set back to the time *Stramonita* appeared.

Finally, it is nearly impossible to determine the geological origin of a genus prior to knowing which species should be included in that genus; the record of a genus may be based on a geologically younger species (e.g. the type), while other (older) members of that genus are incorrectly allocated to another genus.

It is clear—to the dismay of many paleontologists—that the meager fossil record (in this case of the Rapaninae), cannot *a priori* be interpreted with any degree of certainty. Nevertheless, the fossil record is potentially useful. A phylogenetic tree resulting from suites of primarily anatomical, radular, shell ultrastructural, and protoconch characters can be compared to ultrastructural data supplied from the fossil record (for example *Ecphora*). Furthermore, congruence between the phylogenetic hypothesis (tree topology) and the fossil record can then support a cladogram and at least suggest relationships. A detailed study of the shell ultrastructure of fossil Rapaninae and closely related taxa may provide further insight into evolutionary relationships among both extant and fossil taxa.

Congruence of Proposed Phylogeny with Recent Zoogeographical Patterns

A comprehensive study, ideally of monographic nature, based on character suites (such as presented in this study), is necessary prior to determining the zoogeographical range of a genus. Only after questions of relationship among species have been solved, distribution patterns for genera may appear and can be interpreted. For example, the distribution of the genus *Nucella* is far more extensive if some "*Thais*" species from the South African Province are shown to belong to *Nucella s.s.* I predict that many range extensions of genera treated herein will be revised when new limits are set for each genus.

Preliminary geographical patterns for the genera are discussed below, following the branching sequence of the consensus cladogram (Fig. 30).

Clades A, B (Fig. 30): The genus *Nucella* occurs from the eastern Atlantic (northern Europe) to the western Atlantic (northeastern U.S.) Ocean and in the North Pacific (California to the Aleutians to Japan). Preliminary anatomical data (Kool, unpublished data) suggest that the South African muricids, "*Thais*" *dubia* (Krauss, 1848), "*T.*" *squamosa* (Lamarck, 1816), and "*T.*" *wahlbergi* (Krauss, 1848), are ocenebrines; further research may reveal that these species should be placed in *Nucella,* as suggested by Kilburn & Rippey (1982), thus extending the range of the genus *Nucella* considerably. *Forreria* is limited to the North American West Coast. If future studies reveal that this genus is synonymous with *Chorus* Gray, 1847, the range would be extended to northwest South America. The genus *Haustrum* is limited in distribution to New Zealand (some records from Australia). The Recent terminal taxa of Clade A (Fig. 30) live in cool to cold water environments. This similarity in habitat may be considered an additional synapomorphy of Clade A.

Clade C: This clade has representatives from the Atlantic, eastern Pacific, and Indo-Pacific oceans. Only minor patterns can be detected in this clade when superimposing geographic distribution onto the topology of the tree. Most of the genera in the Rapaninae (*Rapana, Vexilla, Nassa, Pinaxia, Drupa, Cronia, Purpura,* and *Mancinella*) have representatives only in the Indian and Pacific oceans. *Rapana* inhabits the Black Sea in addition, but was introduced there by man. *Nassa* comprises at most two species, *N. serta* and *N.* "*francolina,*" the former occurring in the Indian Ocean, the latter in the central and western Pacific Ocean and on the Cocos-Keeling Islands (Maes, 1967). However, these two taxa may be conspecific (see "Remarks" under treatment of *Nassa*). A similar distribution pattern is found in the genus *Drupa: Drupa lobata* (Blainville, 1832), from the Indian Ocean, and *D. grossularia,* from the Pacific Ocean and Cocos-Keeling Islands (Maes, 1967), may also be conspecific. Other species of *Drupa,* such as *D. morum* and *D. ricinus,* occur throughout the Indo-Pacific. Although most species of *Morula* live in the Indo-Pacific, some representatives inhabit the (sub) tropical Atlantic (Kool, unpublished data) and eastern Pacific Oceans.

Cymia tecta, the only living representative of the genus *Cymia* (Clade C, at base, Fig. 30), is limited to the Panamic Province, as are *Vasula melones, Neorapana muricata,* and *Tribulus planospira* (Clade G). Several species of *Stramonita* and *Thais* are known from the tropical eastern Pacific as well, but the type of *Stramonita* occurs in the (sub)tropical eastern and western Atlantic, and so does the type of *Thais.* I suspect that future studies of "*Stramonita*-like" and "*Thais*-like" taxa from the Indo-Pacific may reveal that *Stramonita* and *Thais,* like *Morula,* have an almost global distribution.

The monotypic genera *Concholepas* and *Dicathais* have limited distributions. *Concholepas* is found exclusively in western South America (Chile), while *Dicathais* is endemic to temperate Australia and New Zealand. Fossils of what are believed to be representatives of *Concholepas* have been reported from Australia (Vokes, 1972: 31) and South Africa (Kensley, 1985).

Plicopurpura has one representative in the Panamic Province, and one in the western Atlantic (see "Remarks" under treatment of this genus, and Kool, 1988b). Occurrence of what appears to be a *Plicopurpura* species in Réunion and Mauritius (Drivas & Jay, 1987) is under investigation.

Protoconchs: Reproductive Mode and Phylogenetic Implications

Protoconch morphology has been shown to be indicative, at least to a degree, of relationship and modes of development of gastropods (Shuto, 1974; Jablonski, 1982). A paucispiral, smooth protoconch, with smooth transition from protoconch to teleoconch, is usually indicative and typical of species with a crawl-away larva. A multispiral protoconch with varying degrees of sculpture, outward-flaring lip, and sinusigeral notch for accommodation of the velar lobes, is usually indicative of a planktonic larval phase.

The species used as outgroup in the cladistic analysis, the muricine, *Muricanthus fulvescens,* has the greatest number of protoconch whorls (4.5–4.75), and a pattern of microscopic pustules on most of its whorls, with an outward-flaring lip and sinusigeral notch (Fig. 24C, F). The protoconch of *Nucella* is smooth, paucispiral (about 1.25 whorls), and has a smooth transition into the teleoconch (Fig. 15C, D). In contrast to *Nucella,* all rapanine genera examined have multispiral protoconchs, varying from two to at least 4.25 whorls (completely intact specimens of protoconchs may reveal numbers as high as 4.75), with outward-flaring lip and sinusigeral notch, and with sculptural patterns varying from subsutural plicae to pustulate whorls.

Within Clade D no distinct trend in reduction or increase in number of whorls is visible; some of the highest numbers of whorls occur in Clade F (*Morula, Cronia*). Most rapanine species have three to four protoconch whorls. *Concholepas, Thais, Plicopurpura,* and *Vexilla,* have a relatively low number of whorls, varying from two to about three.

A certain degree of convergence in protoconch morphology is apparent. Although the rapanine protoconch usually has one to three-and-a-half more whorls than the protoconch of the ocenebrines herein examined, *Vexilla* is an exception in having only two whorls. A very high number of whorls is found both in the outgroup and in the rapanines, *Morula* and *Nassa.*

Despite some degree of convergence in protoconch whorl number, the cladogram provides great predictive power for missing data on protoconch morphology. For example, I predict that well-preserved protoconch specimens of the species of Clade G (Fig. 30) will reveal a sculptural pattern as found in most members of Clade E (3–4.5 whorls, with subsutural plicae). The cladogram furthermore predicted that *Haustrum haustorium* has a paucispiral, smooth protoconch, which I found confirmed in Suter (1913) prior to the final computer analysis. Scanning electron micrographs will reveal if the protoconch of *Haustrum haustorium* lacks an outward-flaring lip and sinusigeral notch, as suggested by the cladogram. The protoconch of *Cymia* is more difficult to predict because of its position between the ocenebrine clade (Clade A, Fig. 30) and the remaining members of the rapanine clade (Clade D).

Evidence obtained from protoconch morphology indicates that all members of the Rapaninae studied herein (Clade C, Fig. 30) probably have planktonic larvae. It has always been believed that rapanine ("thaidine") gastropods displayed two very different modes of development: lecithotrophic (direct) and planktotrophic (indirect). For example, *Nucella,* traditionally included in Thaididae/nae of authors, has direct development with "crawl-away" hatchlings (Ankel, 1937; Spight, 1979) and lays egg capsules containing nurse eggs (Spight, 1979). However, as shown previously (Kool, 1993), *Nucella* is to be excluded from Rapaninae and to be included in Ocenebrinae. It is now clear that a planktonic larval stage is typical for Rapaninae and that the direct mode of development is a synapomorphy for Clade B (Fig. 30) and, perhaps, for Clade A if *Haustrum* is revealed to be lecithotrophic.

It should be noted that although one basic protoconch type is present in the Rapaninae (multispiral and [usually] sculptured), and another in the Ocenebrinae (paucispiral and smooth), protoconch morphology varies greatly within the Muricinae. Therefore, depending on which muricine species is used as outgroup, the character state "multispiral" is either the apomorphic or the plesiomorphic condition. Perhaps the muricine outgroup should be coded "either multispiral, sculptured or paucispiral, smooth" in future analyses.

Phylogenetic Relationships Between Rapaninae and Other Muricid Taxa

In this study two taxa were examined in less detail (*Acanthina* and *Trochia*). Some of the data on these lesser-understood taxa indicate or, at least, suggest their relationships with the taxa studied in detail. An "incomplete" and sometimes scattered data base based on anatomical, radular, protoconch, opercular, and shell ultrastructural characters, yielded several conclusions about phylogenetic relationships between taxa studied in detail and those within the Muricidae.

For example, a few anatomical, protoconch, and shell ultrastructural data suggest that *Acanthina* is very closely related to *Nucella* and should also be excluded from Rapaninae. *Nucella* and *Acanthina* both appeared in the Miocene, and *Acanthina* also occurs in cold to temperate waters (California—North Mexico, Chile), and overlaps in geographic range with the range of *Nucella emarginata* (Deshayes, 1839).

The monotypic genus *Trochia* from South Africa, with a paucispiral protoconch of about 1.5 whorls (Fig. 28C, D), and similar to *Nucella* in shell ultrastructure (Fig. 15C, D), should also be excluded from Rapaninae. Results from future anatomical studies may reveal justification for synonymization of *Trochia* with *Nucella*. Kilburn & Rippey (1982) referred the nominal species, *cingulata,* to *Nucella* instead of *Trochia.* Egg capsule morphology, however, differs greatly among *Trochia cingulata* and members of *Nucella* (Kilburn & Rippey, 1982; D'Asaro, 1991).

Forreria (Fig. 26A–F) may be closely related to the genus *Chorus,* an eastern Pacific genus from the Chilean waters. Future studies may show that *Chorus* and *Forreria* are merely synonyms. Both genera have a labial tooth (a structure also found in *Acanthina*), and have a very similar, distinct shell shape.

The fossil genus *Ecphora* (Fig. 29A–E), has been allocated to different muricid families [Rapanidae (Wenz, 1941); Thaididae (Petuch, 1988, in Ecphorinae Petuch); Muricidae (Ward & Gilinsky, 1988)]. The protoconch of *Ecphora* cf. *quadricostata* (Say, 1824) (Fig. 29C, D) is multispiral and counts about three smooth whorls, similar to *Cronia* and *Dicathais,* but lacks an outward-flaring lip and sinusigeral notch as does, for example, *Nucella.* Based on these criteria it could belong to either the Ocenebrinae or the Rapaninae. The shell ultrastructure consists of an aragonitic layer with crystal planes oriented perpendicular to growing edge (15–30%), an aragonitic layer with crystal planes oriented parallel to growing edge (25–35%), and a calcitic layer (45–55%) (Fig. 29E). This type of shell ultrastructure is found in *Nucella* and related taxa, such as *Trochia* and *Forreria,* but also in *Concholepas* and *Dicathais.* The shell of *Ecphora* (Fig. 29A, B) bears resemblance to both the ocenebrine *Trochia* (Fig. 28A, B) and the rapanines *Dicathais* (Fig. 9A, B) and *Rapana* (Fig. 25A). However, based on the absence of an outward-flaring lip and sinusigeral notch, I place *Ecphora* provisionally in the Ocenebrinae.

The protoconch and radula of *Urosalpinx cinerea* (Say, 1822) (Fig. 27E–G) are very similar to those of *Nucella* (Fig. 15C–F). Further studies of *Urosalpinx* species are likely to confirm a close tie with *Nucella.* Although *Urosalpinx* lacks a calcitic outer layer (Petitjean, 1965), it may belong in a clade with *Nucella, Acanthina, Trochia,* and *Forreria.*

Radular Evolution in the Rapaninae

Patterns of rapanine radular morphology are not usually congruent with present taxonomic classifications of rapanines and closely allied muricids (Bandel, 1984; Fujioka, 1985; Kool, 1987), because these classifications are based solely on shell morphology and are thus unreliable (see INTRODUCTION). Now that monophyly has been established for the Rapaninae, patterns in radular morphology can be discussed against a phylogenetic background. Comparisons between findings presented here and reports from the literature are discussed below in an order reflective of the branching sequence in the cladogram (Fig. 30).

Clade A: Troschel (1866–1893) included *Haustrum haustorium* in the genus *Polytropa* (= *Nucella*), based on the width of the rachidian tooth. Cooke (1919) pointed out that the rachidian tooth in *Haustrum* (Fig. 11D) is very different from the rachidian found in *Nucella* (Fig. 15F) and *Forreria* (Fig. 26E), and suggested that either *Haustrum* was the "progenitor" of the *Thais* and *Nucella* groups (making a clear distinction between the "*Nucella*" group and the "*Thais*" group [pp. 103, 109]), or was derived from one of them. Later in the same paper, he stated that *Haustrum* is primitive. Troschel (1866–1893) suspected a close tie between *Nucella* and *Acanthina* but proclaimed separate generic status for both taxa. The position of *Nucella, Acanthina* and *Haustrum* on the cladogram (Fig. 30) is largely congruent with both Troschel's and Cooke's conclusions.

According to Cooke (1919) and Wu (1968) there are some similarities between the bases of the rachidian teeth of *Morula* and *Nucella,* suggesting a relatively close tie between these two genera. Bandel (1984) noted close similarity between the radula of *Ocenebra erinacea* and a *Morula* radula depicted by Cernohorsky (1969). These conclusions are not supported by the branching pattern in the cladogram. Kool (1993) has shown the high degree of similarity in radular morphology between *Ocenebra* and *Nucella.*

Clade C: Cymia (Fig. 8H) is considered a "link between *Morula* and *Thais*" by Cooke (1919) who based this conclusion on radular resemblances among these three genera. *Cymia* has a radular morphology somewhat atypical of rapanines and, derived from the cladogram, is the most primitive member of the rapanines examined herein.

Tanaka (1958) deemed the rachidian tooth of *Rapana* (Fig. 25C) to be very similar to that of *Purpura* (Fig. 18D). I do not agree; the rachidian of *Rapana* has three large cusps and no marginal area, or marginal cusp, whereas *Purpura* has a wide marginal area with well-developed denticles and a pronounced marginal cusp.

Clade D: Troschel (1866–1893) placed *Nassa* (Fig. 13G) close to *Plicopurpura* (as "*Patellipurpura*") (Fig. 17E), based on rachidian tooth morphology. Cooke (1919) disagreed, placing *Nassa* close to *Vexilla* (Fig. 23C). Furthermore, Cooke (1919) placed the genera *Rapana, Concholepas, Pinaxia,* and *Drupa* close to *Thais.* I agree with Cooke on the close evolutionary relationship between *Nassa* and *Vexilla,* and the close ties among the other four taxa, although *Rapana* and *Concholepas* are located at the base of Clade D.

Cooke (1919) considered the morphology of the rachidian tooth in the genus *Plicopurpura* (Fig. 17E) distinct enough to justify separation of this genus (as "*Patellipurpura* Dall") from *Thais* (Fig. 20F) (and, presumably, from *Purpura*). My conclusions are in agreement with those of Cooke (Kool, 1988b). Cooke also stated that the rachidian tooth morphology must be primitive, based on the distribution of this genus (occurring on both sides of the Panamic Isthmus). I do not agree with this statement; the rachidian tooth morphology of *Plicopurpura* is unique and should be considered as derived.

Clade F: Authors generally agree that the rachidian teeth of *Cronia* (Fig. 8D) and *Morula* (Fig. 12G) are extremely similar (Cooke, 1919), and that *Morula* and *Drupa* (Fig. 10C) are more distantly related than their shell morphologies suggest (Cooke, 1919; Emerson & Cernohorsky, 1973). The tree (Fig. 30) and data presented by Kool (1987) show that *Drupa* and *Morula* are not sister taxa.

Clade G: Arakawa (1962) allotted full generic status to *Mancinella,* based on the morphology of the rachidian tooth (Fig. 11I). I agree and recognize *Mancinella* as a full genus. Cooke (1918) proposed the subgenus *Neorapana* under *Acanthina* for *Acanthina muricata.* He considered *Neorapana* to be a close, New World relative of *Rapana* based on radular and shell morphology. (Note: his drawing of a *Neorapana muricata* rachidian tooth does not resemble that of *Neorapana muricata.*)

Fujioka (1985a) suggested from ontogenetic data that a complex pentacuspid ("comb-" or "sawlike") rachidian tooth may be a primitive condition in Thaidinae of authors, whereas a simple monocuspid rachidian tooth may represent a derived condition. He presented a pattern of transformations in radular morphology for several genera and species (including *Nucella* and other non-rapanines). The major drawback of using terms such as "comblike" or "sawlike" or as "pentacuspid" or "tricuspid" is that a division in these categories is artificial and may not reflect homology. Furthermore, they are too general and allow for different interpretations. For example, I would interpret the "sawlike" condition in *Drupa* as more comblike and homologous with the comblike condition in *Purpura;* additionally, I consider the "sawlike" condition in *Drupa* as being very different from the sawlike condition in *Nucella,* or in *Concholepas.*

The cladogram (Fig. 30) is, however, congruent in some aspects with the pattern discussed by Fujioka (1985a). "Sawlike" radula are found in several taxa at the bases of Clades D and E (Fig. 30) (*Rapana, Stramonita, Concholepas,* and *Dicathais*), as well as in the taxa *Nucella* and *Forreria* (Clade B; non-rapanines). Some of the other taxa on Clades E and G have relatively narrow, tricuspid rachidians (*Nassa, Mancinella*), several of which have only small lateral cusps (*Neora-*

pana, Vexilla, Plicopurpura). *Haustrum,* a non-rapanine, clearly has a wide, pentacuspid, but not comblike, rachidian tooth. A more or less comblike condition occurs only in more derived rapanines, such as *Drupa, Purpura,* and *Pinaxia,* and appears to be the derived condition. *Morula* and *Cronia* both have a wide rachidian due to the wide marginal area, but only the central cusp is well developed in these taxa.

Several other authors have attempted to group muricids on the basis of rachidian cusp number (tricuspid and pentacuspid [Arakawa, 1962; Wu, 1965b, 1967, 1973]). However, as is clear from this paper, divisions in Muricidae based on this character, result in para- and polyphyletic groups. Only after monophyly has been established can this character be used to provide a basis for further resolution within clades.

Evolution in Egg Capsule Morphology

Patterns in egg capsule morphology are not obvious. The egg capsules of *Haustrum haustorium,* a non-rapanine, resemble those of the rapanine *Purpura persica,* and the egg capsules of *Nucella* spp. are also similar to those of certain rapanines.

Habe (1960) recognized two different types of egg capsules in muricids: (1) vase-shaped or pillar-shaped, with a short stalk (e.g. Fig. 6A), and (2) lenticular, with a broad base. He included several species from the Muricinae, Thaidinae (of authors), and two species of the Rapaninae (of authors) in the first category, other muricids (trophonines etc.) in the second. This division is too simplistic, and numerous exceptions can be found (for example, *Purpura bufo* and *Thais deltoidea* have egg capsules with broad bases and lack a stalk).

Bandel (1976) provided a phylogenetic hypothesis for evolution of egg capsule morphology, after recognizing different "Formengruppe." He placed members of *Nucella, Thais, Stramonita* (as "*Thais*"), and *Rapana* together into one of these categories, exclusive of *Thais deltoidea,* which he placed into a category with members of *Coralliophila.* This indicates a case of convergence in egg capsule morphology.

When the egg capsule morphologies of more rapanine type species, some of which were recently described and illustrated by D'Asaro (1991), become known, a search for overall patterns in egg capsule morphology may reveal certain evolutionary trends.

Systematic Conclusions and New Taxonomic Arrangement

The cladogram (Fig. 30) indicates that Thaididae/nae of authors is paraphyletic and consists of two taxonomic groups: Clade A, comprising *Haustrum, Nucella, Forreria, Acanthina,* and *Trochia;* and Clade C, comprising *Cymia, Rapana, Stramonita, Concholepas, Dicathais, Vasula, Thais, Tribulus, Neorapana, Purpura, Mancinella, Drupa, Plicopurpura, Pinaxia, Vexilla, Nassa, Morula,* and *Cronia.* However, a clear cut-off point for either group is not obvious; some parallelism is evident in several character states found in members of Clade A and in taxa at the base of Clade C (long accessory salivary glands, separate ventral pedal gland [females] and boring organ, very thick outer calcitic layer, lack of posterior seminal receptacles [females]). Furthermore, the tree topology reveals a parallelism in the morphology of the prostate duct [males] (not in open connection to mantle cavity) between *Haustrum* and the members of Clade C. These taxon groups are not sufficiently distinct from one another, nor are they sufficiently distinct from Muricinae to warrant family status for either Clade A or C. I therefore agree with Ponder (1973) that the family Muricidae contains several subfamilies, and that Muricoidea includes, amongst other groups, the Buccinidae and Muricidae.

The taxonomic revision of the Thaididae/nae of authors (Clades A and C, Fig. 30) has important nomenclatural consequences. First, the taxa on Clade A are placed in the Ocenebrinae (Kool, 1993) rather than Thaidinae. Secondly, the higher category name of the taxa in Clade C (the remains of Thaididae/nae of authors) needs to be reevaluated. Because *Rapana* is monophyletic with the other taxa in Clade C (Fig. 30) the name for this natural group becomes Rapaninae Gray, 1853, which has priority over Thaidinae Jousseaume, 1888, rendering Thaidinae a junior subjective synonym of Rapaninae.

The high degree of similarity in radular morphology among *Tribulus, Neorapana,* and *Vasula* of unresolved Clade G (Fig. 30), and the fact that two of these taxa are monotypic, suggests that these taxa should be allotted subgeneric status under *Thais.* Perhaps further studies will justify synonymization of these genera with *Thais. Mancinella* and

Purpura, however, are sufficiently different from the other four taxa and from one another to be conserved as separate genera. In the more resolved output trees, the latter two taxa are separate from the other four, which often form a polytomy in many of the trees.

The polytomous Clade B (Fig. 30) suggests a close relationship among *Acanthina, Trochia,* and *Nucella,* but the low resolution is most likely the result of the lack of morphological data for the former two taxa. Data on the egg capsule morphology of *Trochia* (Kilburn & Rippey, 1982) support separate generic status for this monotypic taxon, but anatomical and/or molecular studies of the South African *Nucella*-like species are necessary before any conclusions can be drawn.

The newly proposed classification for the taxa examined in this study is as follows:

MURICOIDEA Rafinesque, 1815

- Muricidae Rafinesque, 1815
  - Rapaninae Gray, 1853
    [+ Thaidinae Jousseaume, 1888]
    - *Concholepas* Lamarck, 1801
    - *Cronia* H. & A. Adams, 1853
    - *Cymia* Mörch, 1860
    - *Dicathais* Iredale, 1936
    - *Drupa* Röding, 1798
    - *Mancinella* Link, 1807
    - *Morula* Schumacher, 1817
    - *Nassa* Röding, 1798
    - *Pinaxia* H. & A. Adams, 1853
    - *Plicopurpura* Cossmann, 1903
    - *Purpura* Bruguière, 1789
    - *Rapana* Schumacher, 1817
    - *Stramonita* Schumacher, 1817
    - *Thais* Röding, 1798
      - *Neorapana* Cooke, 1918
      - *Tribulus* Sowerby, 1839
      - *Vasula* Mörch, 1860
    - *Vexilla* Swainson, 1840
  - Ocenebrinae Cossmann, 1903
    [+ Ecphorinae, Petuch, 1988
    + Nucellinae Kozloff, 1987]
    - *Acanthina* Fischer von Waldheim, 1807
    - *Ecphora* Conrad, 1843
    - *Forreria* Jousseaume, 1880
    - *Haustrum* Perry, 1811
    - *Nucella* Röding, 1798
    - *Trochia* Swainson, 1840

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APPENDIX 1

Species Examined Thaididae/nae of authors:

- *Concholepas concholepas* (Bruguière, 1789)
- *Cronia amygdala* (Kiener, 1835)
- *Cymia tecta* (Wood, 1828)
- *Dicathais orbita* (Gmelin, 1791)
- *Drupa morum* Röding, 1798
- *Haustrum haustorium* (Gmelin, 1791)
- *Mancinella alouina* (Röding, 1798)
- *Morula uva* (Röding, 1798)
- *Nassa serta* (Bruguière, 1789)
- *Neorapana muricata* (Broderip, 1832) *1
- *Nucella lapillus* (Linnaeus, 1758)
- *Pinaxia versicolor* (Gray, 1839)
- *Plicopurpura patula* (Linnaeus, 1758) *2
- *Purpura persica* (Linnaeus, 1758)
- *Stramonita haemastoma* (Linnaeus, 1767)
- *Thais nodosa* (Linnaeus, 1758)
- *Tribulus planospira* (Lamarck, 1822)
- *Vasula melones* (Duclos, 1832)
- *Vexilla vexilla* (Gmelin, 1791)
- *Acanthina monodon* (Pallas, 1774) *3
- *Trochia cingulata* (Linnaeus, 1771) *3
- *Ecphora* cf. *quadricostata* (Say, 1824) *3

Rapaninae, of authors:

- *Forreria belcheri* (Hinds, 1844)
- *Rapana rapiformis* (Born, 1778) *4

Muricinae:

- *Muricanthus fulvescens* (Sowerby, 1841) *5

*1 Specimens of the type species of *Neorapana* were typical "*Neorapana tuberculata*" (Sowerby, 1835) morphs; it appears that *N. tuberculata* and *N. muricata* are synonyms. *Neorapana muricata* (Broderip, 1832) is the senior synonym of *Neorapana tuberculata* (Sowerby, 1835) (see "Remarks" under *Neorapana*).

*2 The type species of *Plicopurpura* (*Plicopurpura columellaris* Lamarck, 1816) was not examined, but was substituted by its very similar congener *Plicopurpura patula* (Linnaeus, 1758) because well-preserved anatomical material of this species was available (Kool, 1988b).

*3 These taxa were examined to test if synapomorphies present in some taxa could be recognized in these, facilitating taxonomic allocation. Therefore they were only examined for synapomorphic (diagnostic) characters.

*4 *Rapana rapiformis* (Born, 1778) is a typical rapanine, but it is not the type of *Rapana;* it was included in this study because well-preserved specimens were available.

*5 *Muricanthus fulvescens* (Sowerby, 1841) was chosen to represent the Muricinae as an outgroup in the cladistic analysis, because many living and well-preserved specimens were available.

APPENDIX 2

List of abbreviations used in text.

AMS: Australian Museum, Sydney.
ANSP: Academy of Natural Sciences, Philadelphia.
LACM: Los Angeles County Museum.
MGH: Myroslaw George Harasewych.
SEM: Scanning electron micrograph.
SPK: Silvard Paul Kool.
USNM: United States National Museum.
ZMA: Zoologisch Museum, Amsterdam.

APPENDIX 3

Voucher numbers	
Concholepas concholepas	
USNM 706703	Anatomy: Playa Caleta, Chile
AMNH 132968	Protoconch: Catrihue, Tierra del Fuego, Chile
NMNH 857055	Radula: Valparaiso, Chile
USNM 518777	Ultrastructure: Antofagasta, Chile
USNM 706703	Shell: Playa Caleta, Chile
Cronia amygdala	
USNM 836880	Anatomy: Magnetic Island, Queensland, Australia
USNM 836880	Radula: Magnetic Island, Queensland, Australia
USNM 836880	Ultrastructure: Magnetic Island, Queensland, Australia
USNM 795252	Shell: Collaroy, New South Wales, Australia
Cymia tecta	
ANSP 355766	Anatomy: Vera Cruz, Panama
MCZ 302757	Anatomy: Punta Guanico, Panama
ANSP 355766	Radula: Vera Cruz, Panama
USNM 589636	Ultrastructure: Venado Beach, Ft. Knobbe, Canal Zone, Panama
USNM 216294	Shell: Panama City, Panama
Dicathais orbita	
USNM 836862	Anatomy: Botany Bay, New South Wales, Australia
USNM 681578	Protoconch: Omapere, Hokianga Harbour, New Zealand
USNM 836862	Radula: Botany Bay, New South Wales, Australia
USNM 836862	Ultrastructure: Botany Bay, New South Wales, Australia
USNM 618246	Shell: Ulladulla Harbour, New South Wales, Australia
Drupa morum	
USNM 857059	Anatomy: Pago Bay, Guam, U.S.A.
USNM 720340	Protoconch (*D. grossularia*): Garumaoa Island, Tuamotu Islands
USNM 857059	Radula: Pago Bay, Guam, U.S.A.
USNM 857059	Ultrastructure: Pago Bay, Guam, U.S.A.
USNM 672111	Shell: Tongatapu, Tonga Islands
Haustrum haustorium	
AMS no number	Anatomy: Titirangi Bay, New Zealand
AMS no number	Radula: Titirangi Bay, New Zealand
USNM 531495	Ultrastructure: Rangitoto Island, New Zealand
USNM 531495	Shell: Rangitoto Island, New Zealand
USNM 76300	Shell: New Zealand
Mancinella alouina	
AMS no number	Anatomy: Lizard Island, Queensland, Australia
AMS no number	Radula: Lizard Island, Queensland, Australia
AMS no number	Ultrastructure: Lizard Island, Queensland, Australia
USNM 669734	Shell: Pescadores Islands, China Sea
Morula uva	
USNM 857058	Anatomy: Pago Bay, Guam, U.S.A.
USNM 587364	Protoconch: Kwajalein Atoll, Marshall Islands
USNM 857058	Radula: Pago Bay, Guam, U.S.A.
USNM 685003	Ultrastructure: Motu Akaiami, Aitutaki, Cook Islands
USNM 684893	Shell: Aitutaki, Cook Islands

(*continued*)

Nassa serta	
USNM no number	Anatomy: Pago Bay, Guam, U.S.A.
USNM 719808	Protoconch (*N.* "*francolina*"): Nossi Be, Madagascar
ANSP 269309	Larval shell: Gatope Island, New Caledonia
USNM no number	Radula: Pago Bay, Guam, U.S.A.
USNM 631480	Ultrastructure: Gigmoto, Catanduanes Islands, Philippine Islands
USNM 89600	Shell: Samoa Islands
USNM 618429	Shell: Low Wooded Island, N. Queensland, Australia
Neorapana muricata	
USNM 836661	Anatomy: Puerto Peñasco, Sonora, Mexico
USNM 60718	Protoconch: Acapulco, Mexico
USNM 836661	Radula: Puerto Peñasco, Sonora, Mexico
USNM 836661	Ultrastructure: Puerto Peñasco, Sonora, Mexico
USNM 749212	Shell: San Carlos, Sonora, Mexico
Nucella lapillus	
USNM 857053	Anatomy: Kittery, Maine, U.S.A.
USNM 416825	Protoconch: Manchester, Massachusetts, U.S.A.
USNM 857053	Radula: Kittery, Maine, U.S.A.
USNM 857053	Ultrastructure: Kittery, Maine, U.S.A.
USNM 191106	Shell: Shetland Islands, Scotland
USNM 191094	Shell: Balta Sound, Shetland Islands, Scotland
Pinaxia versicolor	
USNM 262193	Anatomy: Ambatoloaka, Madagascar
USNM 709294	Protoconch: Kuri Island, Hawaii, U.S.A.
ANSP 262193	Radula: Ambatoloaka, Madagascar
ANSP 262193	Ultrastructure: Ambatoloaka, Madagascar
USNM 673781	Shell: Mogadishu, Somalia
Plicopurpura patula	
USNM 857056	Anatomy: South Miami Beach, Florida, U.S.A.
USNM 734594	Protoconch: San Blas Islands, Panama
USNM 857056	Radula: South Miami Beach, Florida, U.S.A.
USNM 736748	Ultrastructure: Cozumel Island, Mexico
USNM 662235	Shell: Mujeres Island, Mexico
Purpura persica	
ZMA no number	Anatomy: Krakatoa, Indonesia
MNHL no number	Protoconch: Tjoba, Tidore, Indonesia
ZMA no number	Radula: Krakatoa, Indonesia
ZMA no number	Ultrastructure: Krakatoa, Indonesia
USNM 700108	Shell: Taiohae Bay, Nukuhiva, Marquesas Islands
Stramonita haemastoma	
USNM 857063	Anatomy: Sebastian, Florida, U.S.A.
USNM 597536	Protoconch: Cocoa Beach, Florida, U.S.A.
USNM 857063	Radula: Sebastian, Florida, U.S.A.
USNM 857063	Ultrastructure: Sebastian, Florida, U.S.A.
USNM 597536	Shell: Cocoa Beach, Florida, U.S.A.
Thais nodosa	
USNM no number	Anatomy: Ascension Island
AMNH 5172	Protoconch: Cape Verde Islands
USNM no number	Radula: Monrovia, Liberia
USNM no number	Ultrastructure: Ascension Island
USNM 767917	Shell: Monrovia, Liberia
Tribulus planospira	
LACM no number	Anatomy: Galápagos Islands, Ecuador
USNM 708234	Protoconch: Malpelo Island, Colombia
LACM no number	Radula: Galápagos Islands, Ecuador
USNM 558161	Ultrastructure: Ensenada de los Muertos, Mexico
USNM 678916	Shell: Academy Bay, Isla Santa Cruz, Galápagos Islands
Vasula melones	
USNM 664731	Anatomy: Palo Seco, Panama
USNM 796187	Radula: Marchena, Punta Estego, Galápagos Islands
USNM 664731	Ultrastructure: Palo Seco, Panama
USNM 732982	Shell: Stony Point, Ft. Amador, Panama

Vexilla vexillum	
USNM 836956	Anatomy: Pupukea Beach, Oahu, Hawaii, U.S.A.
USNM 718391	Protoconch: Tulear, Madagascar
USNM 836956	Radula: Pupukea Beach, Oahu, Hawaii, U.S.A.
USNM 836956	Ultrastructure: Pupukea Beach, Oahu, Hawaii, U.S.A.
USNM 622852	Shell: Mauke, Cook Islands
Forreria belcheri	
USNM no number	Anatomy: Off San Francisco, California, U.S.A.
USNM no number	Radula: Off San Francisco, California, U.S.A.
USNM 169034	Ultrastructure: San Pedrao, California, U.S.A.
Collection MGH	Shell: Catalina Island, California, U.S.A.
Rapana rapiformis	
BMNH no number	Anatomy: Ause Major, Mahe, Seychelles
USNM 655026	Protoconch: South Pagi Island, Indonesia
BMNH no number	Radula: Ause Major, Mahe, Seychelles
BMNH no number	Ultrastructure: Ause Major, Mahe, Seychelles
BMNH no number	Shell: Ause Major, Mahe, Seychelles
Muricanthus fulvescens	
USNM 857064	Anatomy: off Cape Canaveral, Florida, U.S.A.
USNM 621380	Protoconch: 30°18′N, 88°34′W, Gulf of Mexico
USNM 857064	Radula: off Cape Canaveral, Florida, U.S.A.
USNM 857064	Ultrastructure: off Cape Canaveral, Florida, U.S.A.
Collection SPK	Shell: off Cape Canaveral, Florida, U.S.A.
Acanthina monodon	
USNM 2778	Protoconch: Valparaiso, Chile
USNM 131004	Shell: Valparaiso, Chile
Trochia cingulata	
AMNH 128952	Protoconch: Sea Point, Cape Town, South Africa
AMNH 128952	Ultrastructure: Sea Point, Cape Town, South Africa
USNM 2752	Shell: Cape Good Hope, South Africa
Urosalpinx cinerea	
USNM no number	Protoconch: Ft. Pierce, Florida, U.S.A.
USNM no number	Radula: Ft. Pierce, Florida, U.S.A.
Ecphora cf. quadricostata	
USNM no number	Protoconch: St. Mary's Co., Maryland, U.S.A.
USNM no number	Ultrastructure: St. Mary's Co., Maryland, U.S.A.
MCZ 263350	Shell: Chancellor Pt., St. Mary's Co., Maryland, U.S.A.

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